No. 6 — On Burmese earthworms of the family Megascolecidae[1]

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INTRODUCTION

This contribution completes publication of results of the author's study of megascolecid earthworms collected in Burma during 1923-1941. Determination of relationships has been seriously handicapped by loss of much unpublished information (as well as of most Burmese collections) during World War II. Since then only a few Burmese specimens have been available and they were considered elsewhere. Collections from several places in India and from other regions have provided some of the desired data. Information now recorded does, however, provide further confirmation for previously published conclusions (cf. Discussion) as to inadequacies of the classical system of the Oligochaeta and as to the great importance, both for taxonomy and phylogeny, of formerly neglected portions of the somatic systems.

SYSTEMATICS
Family MEGASCOLECIDAE

Redefinition of this family (Gates, 1959) excluded several genera. With those exceptions, the family is equivalent to the Megascolecidae of Michaelsen's classification (1921). Excluded genera, all with tubular prostates of ectodermal origin, were transferred to the Acanthodrilidae or Octochaetidae, according to holonephry or meronephry, respectively, of the excretory

systems. *Plutellus*, formerly in the Megascolecidae of Michaelsen or the Megascolecinae of Stephenson (1930), is now in the Acanthodrilidae and will have to be considered in another article.

Genus PERIONYX Perrier, 1872

This classical genus comprises, in addition to peregrine forms that have been carried from the Orient all around the world by man, species endemic in Ceylon, India, Burma, Australia and New Zealand. The gap in the distribution, though not as great as in the case of *Notoscolex* and *Megascolex* (long notorious for morphological heterogeneity and polyphyly), is large enough to invite reconsideration of the status of the genus. Random sampling of a few species descriptions, each much too perfunctory for present needs, shows that somatic structure of the genus would have to be characterized somewhat as follows: Setae, lumbricin anteriorly or perichaetin throughout. Digestive system, with one or two gizzards or none — with calciferous glands of varied or unknown structure in various segments of the region from vii to xiv or without calciferous glands. Vascular system, with paired or unpaired dorsal trunk, with esophageal or latero-esophageal or lateral hearts in region of x-xiii. Excretory system, holomegaphridial or meromeganephridial, or with micronephridia alongside meganephridia posteriorly. Characterization of genital structure might require addition of the following: Prostates racemose and of mesoblastic origin, or tubular and of ectodermal origin. Whether defined as by Stephenson or as by Michaelsen on any one of several occasions, *Perionyx* obviously is a congeries lacking the over-all similarity of anatomical structure that should be expected in species so closely related as to belong together in a monophyletic genus.

Descriptive matter provides a major portion of the generic definition in its terminal classical form: Setae in rings often almost closed. Male pores often approximated in greater or less degrees, and may be very close to the middle line. Spermathecal pores like the male pores often very near the middle line, the last pair in 7/8 or 8/9. Gizzard frequently more or less vestigial, in v or vi. Two pairs of testes and funnels. Such statements, even when incomplete or not misleading, are not definitive. The meroandric *P. rufulus* Gates, 1945, for instance, provides one more example of the folly of defining genera by genital charac-

ters liable to rapid evolutionary modification, except in strict accordance with over-all somatic similarity.

The type species, *excavatus,* is of Indian origin. Accordingly, search for over-all similarity by which the genus must be defined can be restricted, initially at least, to southeast Asian species that are likely to be congeneric with *excavatus.* Unfortunately, most oriental species have been known hitherto only from descriptions of a holotype or of a short series secured at a single site. Some of the types were known to be abnormal and others assumed to be normal are now under suspicion. Some certainly are immature; at least one is much too juvenile to permit recognition of genital characters by which species must be mainly defined and distinguished from each other. Although an occasional type was old enough to have matured sperm, few if any seem to have had the clitellar tumescence that indicates attainment of the breeding stage.

Location of the gizzard is mentioned in previous species descriptions, usually with some additional characterization such as: recognizable only in sections, vestigial, rudimentary, very small, small, moderately large or large but soft. Although presence of a gizzard with some special muscularity and in v or in vi would seem to be required by the generic definition, at least four species lack any vestiges and another is supposed to have one in vii. Some intraspecific variation also is indicated by the literature, both as to presence or absence and as to location in v or vi. The organ probably was often characterized, because of reluctance to damage a type, from its external appearance in a dissection. However, free-hand sections, with scissors or other instruments, sometimes show that external appearances are quite misleading. Such sections of an anterior portion of the esophagus in field-preserved material of *excavatus* provided so much divergence in laboratory records, both as to presence or absence and location that any mention of a gizzard is omitted from the description below. Regardless of how much use the gizzard may prove to have in defining species, the organ obviously cannot provide any such generic characterization as in *Pheretima* and *Eutyphoeus.* Over-all similarity, insofar then as digestive organs are concerned, must be sought in the remaining portion of the system.

Calciferous glands definitely are lacking in many species, according to previous descriptions. Omission of any mention of the glands usually is attributable to lack of interest in recording absence. None have been found in any species examined by the

author. Nevertheless, calcium secreting tissues are present and fine granules or larger concretions have been found, not only in all species that have been available alive but also in others examined not too long after preservation. Calciferous tissues apparently are located, in low irregular ridges or higher folds that may be more or less lamelliform, within a portion of the esophagus centering at xiii. Some interspecific variation in segmental location is indicated in the literature but field-preserved material is unlikely to provide, even from microtome sections, data needed for species characterization. Only a negative character, absence of discrete glands, is available for generic definition. The segment in which the intestine begins was mentioned in many of the earlier descriptions but none of the authors display knowledge of the difficulties attendant on the determination. Considerable variation is obvious and generic characterization, such as for *Euty-phoeus*, certainly is impossible. Much of the intraspecific variation that has been found (cf. *bainii* and *excavatus*) is attributable to a process (considered below) some knowledge of which is needed by biologists who may have occasion to study any perionyx. Evidence for existence of intestinal caeca and typhlosoles or supra-intestinal glands is lacking in the literature and none of those organs were found in the many specimens that have been examined by the author during the last thirty years. Over-all similarity, insofar as the digestive system is concerned, seems to be limited to negative characters.

The circulatory system was considered of no evolutionary importance for the phylogenies on which the classical system came to be based. Hence, older systematic contributions often provide no information about it. Nothing at all is known about the system in three species of *Perionyx*, and for others all that is recorded is position of the last pair of hearts. They are, so far as is known, either in xii or xiii, possibly with very little normal intraspecific variation. The vascular system, except as just indicated, has been found to be macroscopically identical in all species the author has studied. Such invariability, in the circumstances prevailing, invites an assumption of similar uniformity in other species of the genus. However, just as in case of the hearts, normal must be understood.

The emphasis on normality is required because of a regenerative capacity unequalled in earthworms except in the European *Criodrilus lacuum*. Proof that such capacity often is invoked was secured in India. Collections obtained there during a period

of three years contained 150 specimens of *millardi* Stephenson, 1915, with head and 175 with tail regenerates, 499 of *sansibaricus* Michaelsen, 1891, with head and 1200+ with tail regenerates. Each head regenerate still was externally distinguishable from its substrate by differences in pigmentation and segment size. These external stigmata of regeneration were found, in laboratory experiments, to disappear shortly in case of heads but not tails where obvious differences in pigmentation still remain after a period long enough to permit terminal regeneration a second or even a third time. Older cephalic regenerates (according to data obtained from operations in the laboratory, at known levels and under controlled conditions, if substrates were sufficiently mature or later became mature) are externally identifiable by homoeosis of the clitellum and reproductive apertures. After exclusion of all specimens with recent cephalic regenerates (indicated by pigmentation and segment-size differences) from 8 series comprising 117-1235 specimens of *P. sansibaricus* (total, 3252), incidence of homoeotic individuals was found to vary from 6.1 percent to 14.4 percent. Comparison of the anatomy of natural cephalic regenerates (including homoeotics) with that of several thousand experimentally obtained regenerates provided a number of generalizations, some of which are of special importance in the taxonomy of *Perionyx*. Homoeosis, in interest of simplicity and brevity, is indicated by reference to but one of the three species that were studied experimentally, *P. sansibaricus*. This is characterized as follows: spermathecal pores, 3 pairs, anteriorly in vii-ix; clitellum, on xiii-xvii; female pore, median, in xiv; clitellum, on xiii-xvii; male pores, each in a special area or tumescence within a single field, in xviii; gizzard, in v; calciferous widening of esophagus, in xiii; intestinal origin, in xvi; latero-esophageal hearts in x-xii; testes, in x-xi; ovaries, in xiii; spermathecae, with a single stalked diverticulum.

Rapid formation of a new head is possible by any substrate comprising more than the last fifty segments of the original soma. Shorter substrates, in favorable conditions, may also produce a new head.

All organs of a pre-intestinal region of the body may be developed in epimorphic regeneration. Male terminalia always, other genital organs occasionally, are formed during morphallactic reorganization in a proximal portion of the substrate.

Spermathecal pores may be lacking, or unpaired and then in normal location, or at mV, or (only in morphallaxis) in other

unusual position, or paired and then in 1-7 segments (nearly always consecutive) of iii-xii. Spermathecae may be more or less completely bifid when median, normal, adiverticulate or with two or more diverticula. A mature spermatheca with spermatophore projecting to the exterior from the pore may be moved forward unchanged into an apparently epimorphic regenerate. Spermathecae without spermatophores were more or less completely histolyzed during migration. A battery of six spermathecae in normal segmental locations was present only in 3 of 52 thecal regenerates at levels 11/12-17/18.

Female pores may be pre- or intra-clitellar, median and unpaired, paired or lacking even though female gonoducts are well developed, in 1-4 segments (usually consecutive) of vi-xviii. Ovaries may be present in 1-4 segments of v-xvii.

The clitellum may comprise 2-15 of the segments from v to xxvi. It is always annular.

Male fields may be lacking, asymmetrical or symmetrical, in 1-12 of segments ix-xxvi; when more than one is present they are usually in consecutive segments. Male terminalia may be lacking even if one or more male fields are present; when formed they usually are in but one of the segments with a male field.

A gizzard may be lacking (often), of subnormal muscularity, in any of segments iii-vii. A calciferous widening of the esophagus may be lacking (often), longer than usual, in any of segments ix-xvii. Intestinal origin may appear to be in any of segments ix-xxvi. A portion of the intestine in the proximal part of the substrate often loses the characteristic brown coloration and becomes much narrower, often valvular in appearance. Similar narrowing of an anterior portion of the intestine may take place in fasted animals that are not regenerating, or at height of sexual functioning, seemingly because of compression by prostates.

Latero-esophageal hearts may be present in 1-7 of segments vi-xvi, usually in uninterrupted series, usually paired, one of the last pair occasionally lacking. The six major blood vessels (dorsal, ventral, supra-esophageal, extra-esophageal [2] and subneural trunks) are present, and the last-named extends nearly to the anterior end of the regenerate. Rarely, the dorsal trunk is doubled in a short stretch or resolved into a plexus. Smaller vessels and vascular networks usually show differences from species norm. Divergence from that norm is lacking in the excretory system. The nervous system appears to be normal macro-

scopically, except in monstrosities. The brain of short heads regenerated at really posterior levels may be in ii or i.

Testes may be 1-5 pairs in segments iv-xv. The gonad series usually is uninterrupted in longer regenerates. Testis:ovary ratios usually are divergent from species norm (4:2), for instance, 2:2 in shorter regenerates, 2:6, 6:6, 8:8, 10:2, 10:6, etc., in longer regenerates. Gonads in a middle portion of the series may be hermaphroditic. Sperm and mature ova have been found in the same segment. Female gonoducts may unite in the parietes to open by a single median pore or may acquire individual apertures. Female gonoducts that do not acquire external openings in the segment behind the septum bearing the funnels may turn laterally and join the male gonoducts. Ducts from male funnels may unite in the parietes and open to the exterior through a median aperture indistinguishable from the female pore. (Number and location of ovaries accordingly cannot be determined from position of female pores as sometimes has been assumed.) Some homoeotic individuals not only had matured sperm profusely but in spite of markedly aberrant anatomy had copulated successfully as was proved by presence of sperm in the spermathecae. Aclitellate homoeoties, mature enough to have sperm on their male funnels, also had copulated. Ovaries with apparently mature ova occasionally were found in homoeoties in which no slightest race of clitellar development was recognizable.

Regeneration, in either direction, is possible from the day the young worm emerges from the cocoon. Homoeosis of male field rudiments in juveniles too young for other genital structures to be recognizable may have resulted from regeneration at an earlier stage.

Permutations and combinations of structure, as indicated above, are so numerous as to indicate, especially when finer structure is taken into consideration, that few head regenerates will be identical. Certainly little uniformity was found in regenerates formed at the same level in the laboratory by worms of as near the same age and condition as could be determined by external inspection under anesthesia.

The somatic anatomy that now appears, from normal worms, to be uniform throughout the genus also characterizes regenerates whether cephalic or caudal. Divergence from species norms in the regenerates is very largely restricted to structure by

which species must be identified, defined and distinguished from each other.

In concluding this brief statement of regenerative capacity one of the records illustrative of the remarkable viability of a perionyx is cited. A worm that escaped from its container sometime after the laboratory had been closed for the night was coiled up, the next morning, in full glare from an unclouded hot-season tropical sky. The body was stiff but not brittle enough to break on slight bending. After a few moments in water the anterior half began to jerk back and forth convulsively. Movements shortly ceased and the worm was then placed on a saturated towel in a tightly closed container. The next day, anterior and posterior portions (no indication of autotomy anywhere) were flattened, almost liquefied, giving off an odor that testified to certainty of advanced decay. A middle portion had not yet collapsed and appeared to be normally turgid though unresponsive to slight stimuli. Dead portions were excised so as to leave a fragment (of 22 segments) which in three weeks produced a head regenerate of thirteen segments, anteriorly, and a tail regenerate, posteriorly.

Excretory organs, not even mentioned in descriptions of several species, usually were said to be meganephridial, sometimes with an additional notation such as, "nephridia end in the same line." *Perionyx* has been defined, in effect at least, for 65 years as meganephridial. Hence, mention of a generic character in a species description presumably was not always thought to be necessary. Presence of micronephridia in addition to large nephridia usually has been mentioned in other genera. The only instance in *Perionyx* (cf. *annulatus* below) needs no further consideration here. The excretory system in *Perionyx* now appears to vary interspecifically only with reference to location of nephropores and shape of the vesicles when they are present. The only exception, as to number per segment, is provided by Himalayan giant forms (cf. *annandalei* below).

"Meganephridial" originally meant presence per segment of two nephridia each with a preseptal funnel and a postseptal looped tubule opening in its own metamere to the exterior through an epidermal aperture. An excretory system composed of such units, in modern terminology, is holonephric. The Himalayan giants have several nephridia per segment. These, however, are not micronephridia but are of the same kind as the paired nephridia of other species. The two kinds, in modern terms, are

distinguished from each other as meromeganephridia and holomeganephridia. Difference in number does not appear at present to warrant even subgeneric separation in view of the over-all similarity of somatic anatomy.

Large enteronephric meronephridia — especially when paired as in *Lampito*, and the larger median member of a transverse row of nephridia — as in the post-typhlosolar segments of *Eutyphoeus*, often have been called meganephridia. That term, in the definition below (p. 216), is replaced by a more precise characterization in the hope of avoiding some of the confusion that has prevailed in the past.

The meronephry of the Himalayan giants is assumed to have arisen by longitudinal splitting of each of the two embryonic anlagen per segment. Such splitting, when restricted to preseptal portion of the anlage, presumably has been responsible for the multiple funnels that are recorded from various genera. True integumentary micronephridia arise in another way, by transverse fragmentation of the postseptal portion of the embryonic tubule, and hence are astomate. Such micromeronephridia are so different from meromeganephridia in morphology, ontogeny and phylogeny as to indicate relationships to other genera than *Perionyx*.

Passage of nephridial ducts into the parietes, on each side of the body, in a single more or less regular line may not be proof that external apertures are in a single rank. In certain lumbricids, for instance, some of the ducts open well lateral to the level at which they enter the musculature. Information is needed for species characterization not only as to real locations of the nephropores but also as to presence of vesicles and their shape — in one species the shape appears to vary according to the level at which the pore is located.

Generic uniformity in reproductive systems is restricted to the racemose prostates characteristic of the family and, possibly, median union of oviducts. The classical definition says, "Female pore unpaired (? always)." The parenthetical question presumably refers to *P. foveatus* Stephenson, 1914, in which pairing was suspected though actual pores were not seen. Oviducts in regenerates occasionally do not unite. Coelomic cavities of testis segments in *Perionyx* are filled, at maturity, with a very sticky material that hardens into a firmly coherent mass on preservation. Masses of such coagulum, even in microtome sections and in various species of several genera, have been mistaken for semi-

nal vesicles. A horseshoe-shaped mass of coagulum adherent to the anterior face of 10/11 in *koboensis* Stephenson, 1912, may have been mistaken for a pair of dorsally united seminal vesicles. Loosened peritoneum adherent to the coagulum conceivably could have appeared to be the wall of a testis sac in several species. Male genital apertures rarely have been seen, and are not even in clefts or grooves that were thought to be the male pores. The real situation in *excavatus* was found only when tension on adjacent epidermis separated tightly apposed lips.

Pigment in all species that have been seen alive is red, though the dorsum sometimes appears to be dark blue or even almost black. A green color that may be characteristic of two species is not localized (as also in several species of *Pheretima*, *Eutyphoeus* and *Allolobophora*) in visible granules. The green color shortly disappears in alcohol and in formalin.

Characters that have been found, regardless of species, to be uniform in regeneration homoeotics as well as in normal individuals are assumed to be generically definitive. Lack of information for species that have been unavailable requires the revised definition below to be labelled tentative for the present.

A hypothetical ancestral protoperionyx from which extant species might have evolved is characterized as follows : Prostatic, female and spermathecal pores minute and superficial. Dorsal pores present from 1/2. Digestive system with a gizzard in v and intestinal origin in xii. Excretory system holonephric, without cephalization. Holandric. Seminal vesicles in ix-xii. Spermathecae, without seminal chambers or diverticula, two pairs, opening at 7/8-8/9. Other characters as in definition below.

Absence of calciferous glands, intestinal typhlosole, caeca and other glands presumably is primitive, and most of the gut has remained in that condition throughout the genus. Absence of a gizzard, in some species, may be an illustration of secondary simplification, as classical authorities seem to have agreed that presence of the organ is "a primitive feature in all families of the Megadrili." Retention, without modification, of typical holonephridia in ii and the next few segments also appears to be primitive, at least in comparison with many of the genera now or formerly included in the Megascolecidae. If a complete series of dorsal pores is primitive, there has been very little cephalization of that system in *Perionyx*. Major blood vessels are the same as in *Pheretima* but so little is known about the comparative anatomy of the vascular system in earthworms that only presence

of uninterrupted dorsal and ventral trunks can be called primitive. Absence of spermathecal diverticula appears to be primitive, as also in the Moniligastridae and the Oenerodrilidae. The only specialized characters imputed to the protoperionyx are the perichaetin setae (shared with an ancestral pheretima) and the peripheral union of female gonoducts (probably not shared).

Intrageneric evolutionary developments can be summarized as follows: Transfer of gizzard into vi (common), possibly later on into vii (once?); weakening of the muscles (even when the layer is thick) if the primitive organ really was strong; decrease in thickness of the circular muscle layer (very common) ending eventually (several times) in disappearance of the gizzard. Elongation of the esophagus (common), perhaps in association with posterior extension of calciferous tissues. Addition of a pair of hearts in xiii (independently in Burma, the Deccan, and in the Himalayas). Separation of each nephropore rank into a dorsal and a ventral rank (four times in peninsular India, once in the Himalayas). Increasing irregularity in the single rank may indicate an early trend in direction of the two-rank condition. Enlargement of an ectal portion of the nephridial duct into a vesicle (in three of the peninsular species with nephropores alternating irregularly between two ranks, once in a Himalayan species without alternating pores). Increase in number of nephridia (once, in the Himalayas).

Testes and male funnels of x have been eliminated (once, Assam). Seminal vesicles of ix have been eliminated in all species except *minimus* Stephenson, 1920, those of x in all except *koboensis*, those of xi in *rufulus*. Small chambers have appeared in an ental portion of the spermathecal duct of various species (and perhaps more commonly than has been recognized). They are single and of no fixed position, few and scattered, or in rosettes, bands and rings. One or two stalked diverticula with single seminal chambers have appeared (once each in Burma, the Deccan, South India, possibly in the Malay Peninsula, twice in Ceylon). Better known, of course, because of their use in identification of species, are the changes in number of spermathecae. Addition of a third pair in vii (4 species in the Himalayas, 3 in peninsular India, 1 in Ceylon), elimination of the pair in ix presumably after acquisition of the pair in vii (16 species in the Himalayas, very little known about any of them). Elimination of the pair in ix before a pair had been acquired in vii (2 species, Burma). Acquisition of a pair in vi,

presumably after appearance of a third pair in vii (2 species, Burma). One species in Ceylon is supposed to have seven pairs of spermathecae but a hyperplasic battery may have resulted from regeneration. Intermediate stages, of five and six pairs are unknown and the octothecal condition is found only in Burma.

Other changes in the genital system: evolution of intromittent copulatory organs, at least twice (in 3 Himalayan species); evolution of penial setae of a rather generalized type (common); elimination of penial setae (or at least of ventral setae that could have been penial); migration of spermathecal and male pores laterally or mesially; dislocation of spermathecal pores back from the intersegmental furrows (once in the Himalayas, once in the Deccan).

Macroscopically recognizable evolutionary changes, as now known, obviously are much more numerous in the genital than in any other system. Some of the changes may have been made independently in two or more portions of the generic range. Unfortunately, much more information about somatic systems of inadequately characterized species is needed for determination of present and past relationships. Primitive forms certainly live, in the Himalayas, alongside forms that have specialized intromittent organs, an advanced sort of meronephry, modified spermathecal batteries, much larger numbers of setae, and considerably greater soma size. The Himalayas, or more precisely an eastern portion, were thought (Stephenson, 1923, p. 27) to be "the great focus of evolution of species of *Perionyx.*" That focus may prove to be part of the area in which the genus originated, for direct derivation from the Australian *Diporochaeta*, as in classical phylogenies, is impossible. Migration, according to available evidence could be only to the west along the Himalayas and to the south through much of Burma and most of India. Absence of endemics in the Gangetic valley suggests passage from Assam-Burma to the Indian peninsula across the "Garo-Rajmahal gap" (where earthworms ought to be collected intensively at the earliest opportunity). However, paucity of colonizations by peregrine forms in the valley may indicate that conditions have become unfavorable to worms with special ecological requirements. Whether Ceylon and the Malay Peninsula were reached without assistance by man remains to be learned.

The single evolutionary trend that has been recognizable throughout the whole genus is derogation of the gizzard. Vestiges may still be identifiable microscopically even in the very few species that were supposed to be gizzard-less. Presumably then, elimination of the gizzard may require much more time than classical authorities believed, for during the period in which thickness of the circular muscle layer was decreasing, more profound changes were made in the genital system such as elimination of a pair of gonads, of a pair of spermathecae or addition of one or more pairs of spermathecae.

Tentative definition of Perionyx. Digestive system, without supra-intestinal and calciferous glands, intestinal caeca and typhlosole, but with calciferous tissues in some portion of the esophagus. Vascular system with complete, unpaired, dorsal, ventral and supra-esophageal trunks, a subneural adherent to the parietes, paired extra-esophageal trunks median to the hearts, latero-esophageal hearts in x-xii. Nephridia with preseptal funnels and postseptal loops that open to exterior in their own segment through epidermal apertures. Setae, numerous, in a circle at equator of each segment from ii posteriorly. Female pore intraclitellar and median. Clitellum, annular, setae retained. Spermathecae pregonadal. Ovaries fan-shaped and with several egg strings. Prostates, racemose, of mesoblastic origin, with ducts joined entally by the vasa deferentia.

Characters that may prove to be uniform throughout the genus: abortion of septa restricted to region in front of v, no septa thickly muscularized; pigment, red; gizzard (when present) in front of 6/7; definite copulatory papillae lacking (genital markings lacking except for modifications of male field and epidermal tumescences in vicinity of spermathecal pores).

Distribution. Burma, Assam, the Himalayas west at least to Simla, peninsular India, possibly also Ceylon and the Malay Peninsula. The original home of *violaceus* Horst, 1893, supposedly in the peninsula, is unknown. The species has been found in the West Indies. (Distribution of three species widely transported by man not included, above.)

PERIONYX ANNANDALEI (Michaelsen, 1907)

Redefinition of *P. m'intoshi* (Gates, 1952, p. 7) left other giant forms in need of a name. The earliest name that may be available is *Perionychella annandalei* Michaelsen, 1907. The

nature of the excretory system in the type of that species unfortunately is unknown. The only data that might contra-indicate identification with the Nepalese giants are penetration of prostates into xix, and location of male pores in the setal circle rather than posteriorly. If *annandalei* proves to be specifically distinct, *Lampito dubius* Stephenson, 1916, may be available. The holotype of that species (from Darjiling district) is meronephric and male pores are in a transverse groove behind the setal zone as in the Nepalese worms. The type, only 6 mm. thick (10-15 mm. in sexual giants) and with spermathecae still confined to the parietes, is too juvenile for recognition of important taxonomic characters.

Male terminalia of two Nepal Valley specimens, originally referred to *m'intoshi*, are one segment behind their normal location and are in xix. Other organs may have been in their normal situations. If so, the aberrant condition, it is now clear, could have arisen in several ways. 1) By mutational translocation of developmental potentiality back into somites at the 19th level. 2) By halving of a mesoblastic somite on each side of the body, at any of the 14th to 17th levels. 3) Somite halving on one side and mutational translocation on the other is theoretically possible. 4) As a result of cephalic regeneration (in a variety of ways depending on level of regeneration, age of regenerant and whether or not morphallaxis also is involved). If gonads are hyperplasic, regeneration is very probable and also morphallaxis. The aberrant worms, in less fortunate circumstances, could have become types of a new species defined by location of male terminalia in xix. Indeed, a distantly related Bombay species, *P. pullus* Stephenson, 1920, is known only from the original description of a single individual that does have male terminalia in xix. However, the specimen was believed to be abnormal, but only with respect to location of the terminalia. If regeneration was responsible for the homoeosis, supposedly normal organization could have been divergent from a specific norm in one or more of several ways. A gizzard, for instance, is lacking, but that structure often is not developed in head regenerates of species that have a much greater musculurity of the organ than in most perionyxes. The spermathecal battery could have been defective or even hyperplasic. Although regeneration now seems to be the most probable cause of the *pullus* homoeosis, another possibility must not be overlooked — that location of the male terminalia in xix is a specific character.

Translocation does occur in mutant individuals of another genus, and in the H morph of *Pheretima anomala* male terminalia are in xx.

(PERIONYX?) ANNULATUS Stephenson, 1914

This species is known only from the description of six specimens from two localities. Four were juvenile; one was regenerated posteriorly, one damaged anteriorly (and not described), another much softened, the last homoeotic (male pores in xix). The clitellum of one adult probably is not tumescent though sperm were present on male funnels. The other adult is homoeotic (male pores in xx). The macerated and supposedly normal adult is the one from which the species was defined. *P. annulatus* differs from all oriental perionyxes in the location of the gizzard behind 6/7 (in vii) and in the presence of "a number of minute micronephridia in regular transverse lines, especially ventrally, in the neighbourhood of the meganephridia." Although *Perionyx* was defined as meganephridial, this species was included (without change in generic definition) because "its general habitus is so markedly that of *Perionyx* that it can hardly be doubtful where its relations lie" (Stephenson, 1914). The regenerative capacity (cf. below) that is indicated by the homoeoties also appears to be markedly that of *Perionyx* and hence much greater than in any other oriental genus. Habitus, together with regenerative ability, justify a question as to whether supposed micronephridia really are excretory organs (cf. *excavatus*). Minute, parietal micronephridia in oriental earthworms are astomate, v-shaped and exonephric. If such nephridia are present in *annulatus* the species obviously does not belong in *Perionyx*. If the supposedly normal mature worm had regenerated, as is quite possible though the text provides no evidence for it, gizzard location could be abnormal (as often in cephalic regenerates) and the spermathecal battery could be hyperplasic. If the battery is quadrithecal normally, and especially if the gizzard really belongs in vii, relationships to *m'intoshi* would appear to require consideration.

The abnormalities which include hyperplasic spermathecae and gonads of both sexes, as well as heterogeneous organ homoeosis (e.g., last hearts +2, male terminalia +1, in the juvenile), now are known to arise during cephalic regeneration, which in the present instances may have been at some level behind 13/14 and in part morphallactic. Accordingly, at least

fifty per cent of the worms that were available had regenerated. Half of the adults and a third of the series had regenerated anteriorly.

At least two other species are presently known only from original descriptions of short series that contained homoeotic individuals. *P. turaensis* Stephenson, 1923, was erected on five specimens. All organs from spermathecae to male terminalia of one individual are two levels in front of normal location. The homoeosis undoubtedly resulted from hypomeric cephalic regeneration (-2) at some level in front of 10/11. *P. rufulus* was erected on 11 specimens two of which are clitellate. One of them is homoeotic, doubtless as a result of hypomeric regeneration (-1), possibly at 10/11.

<div align="center">PERIONYX BAINII Stephenson, 1915</div>

<div align="center">India</div>

Almora, United Provinces, in wet ground below spring, *ca.* 6000 feet, June, 0-0-15.

Simla, July, ?-2-50. M. Mathur. (100 odd juveniles, quite probably are of the same species.)

External characteristics. Size, 35-55 by 3-4+ mm. Segments (5 specimens), 91-110. Pigmented, dorsum red or apparently dark blue, ventrum in i-iv or v often light red. Prostomium epilobous, tongue open (37 specimens), definitely closed (1), doubtful in others because of presence of slight and possibly adventitious furrows (one such at mD in prostomial tongue may reach to or well towards 1/2 but always is much less marked than in *sansibaricus*). Setae more closely crowded ventrally; viii/11-15, xix/11-13. Nephropores probably in one somewhat irregular rank on each side, at or close to mL. Clitellum, annular, on xii-xviii, much thinner on xvii and xviii, lacking in ventrum of xviii.

Spermathecal pores large, transverse slits, exactly on intersegmental furrows. Female pore presetal at mV. Male pores small, longitudinal slits at segmental equator, just lateral to penial setae, each overhung by a small but definite and rather spheroidal to ellipsoidal tubercle that must be drawn laterally before the pore can be seen. Median to each male pore, tips of 5-9 penial setae are visible, in a circle or in two transverse rows convergent mesially and laterally, sometimes in a shallow, transversely slit-like depression. Male field quite variable in appearance. Four greyish translucent areas usually recognizable

median to the male pores, two presetal and two postsetal. The whole field may be depressed and with a tubercle-like tumescence on each lateral wall.

Internal anatomy. Longitudinal muscle band at mD densely pigmented. Pigment, regardless of external appearances, always red. Postclitellar septa without noticeable thickening (22 specimens). Gizzard rudimentary, in v (22). Esophagus much widened and bead-like in xiii, with calciferous ridges on inner wall. Intestinal origin in xv (8), in xvi (14). No typhlosole (22). Circulatory system as usual, the subneural trunk sometimes recognizable as far forwards as iii. Last hearts in xii (22). Nephridia avesiculate, ducts long and slender, passing into parietes in a single rather irregular rank on each side of the body.

Posterior seminal vesicles, not united dorsally, appear to extend into xiii or xiv with ventral margins incised by the septa. Male gonoducts, which pass into ental ends of prostatic ducts, may be along ventral margin of the prostate or imbedded apparently within the gland itself. Penial setae with 9-11 rather irregular and occasionally interrupted circles of elongately triangular spines. The tip appears pointed as the seta rests normally on the slide, often convex on one side and flat or slightly concave on the opposite side. When the shaft is rolled over, the tip appears to be chisel-shaped or truncate, or the terminal margin may be roughened or even slightly indented to a somewhat bifid appearance.

Spermathecae large, reaching into contact with the dorsal blood vessel or even to dorsal parietes. Seminal chambers unrecognizable externally and not seen in free-hand sections of the duct.

Abnormality. Ten of the Almora worms, larger than the others, are athecal. Seminal vesicles are small, vertically placed, on posterior faces of 10/11-11/12. Prostates (9 worms) perhaps slightly smaller than in thecal individuals. Male pores, prostates and their ducts, lacking in the tenth worm in which male deferent ducts had not grown back into xviii. Setae of xviii ventrally are arranged into two discrete groupings just as in normal worms but other portions of a male field are unrecognizable.

Mesoblastic anlage of the prostates may have developed sufficiently to be able to induce rearrangement of follicles that eventually would have become penisetal but only to abort

before the male gonoducts in their posterior growth, had reached xviii. Deprived of the attracting stimuli from the prostatic anlage, the gonoducts apparently ceased to grow.

In the current terminology of genital polymorphism, one third of the Almora batch belongs to some sort of H morph, possibly a male sterile one, 60 per cent to an A morph, the remaining specimen to an AR morph. In *Pheretima*, A and AR morphs, so far as is now known, have evolved only after acquisition of ability to reproduce parthenogenetically. Most A and AR morphs are male sterile. Except for the date above, there is no reason for suspecting parthenogenesis in species of *Perionyx*.

Reproduction. Spermatozoal iridescence was lacking on male funnels and in spermathecae of each specimen. Such absence, in clitellate individuals of *Pheretima* would justify an assumption not only of parthenogenesis but also of male sterility. The juvenile condition of the seminal vesicles would provide further support for the assumption. The coagulum usually present in coelomic cavities of x-xi in sexually functioning individuals also was lacking. Neither lot was secured in the season when species with a limited reproductive period (usually toward the end of the monsoon) breed. However, the species that now seems to be most closely related to *bainii* does reproduce throughout the year or at least so much of it as conditions or environment permit.

Regeneration. Anterior amputees and recent anterior regenerates were lacking. Two of the 52 Simla adults (3.8%) were homoeotics, and without the usual external stigmata of epimorphic (these shortly disappear) or morphallactic regeneration. The internal anatomy of the worms and present knowledge of regenerative capacity in other species of *Perionyx* (Gates, 1951, and MSS) permit several interesting deductions, confirmation of which can be expected. 1) Both worms had regenerated anteriorly; one, a head of 9 segments at 7/8; the other, a head of 14 segments at 15/16. 2) Equimeric regeneration is possible at each level back to 14/15. 3) Head regeneration is possible in *bainii* at each level back at least to region of 50/51 and probably much further posteriorly. 4) Reproductive organs, including spermathecae, testes and ovaries, are developed, in appropriate conditions, in head regenerates. 5) A regenerated head, in certain circumstances, will have no spermathecae and/or male terminalia.

6) Vestiges of the male terminalia, similar to those of the abnormal Almora worm characterized above, develop morphallactically during or after regeneration.

Many of the worms, prior to collection, had lost a posterior portion of the body, apparently at an intersegmental level in each case: 25 per cent of the juveniles, 34 per cent of the clitellates, 100 per cent of the aclitellates. Healing of unregenerate worms had been enteroparietal. Numbers of the worms had regenerated posteriorly; 16 per cent of the juveniles, 24 per cent of the clitellates, 50 per cent of the aclitellates. In each case the regenerate was caudal. Level of regeneration ranged from 39/40 to 87/88 in the juveniles, from 32/33 to 93/94 in the adults. Segment number in those regenerates in which rapid growth had come to an end was: 22 at 39/40, 23-35 at 54/55-58/59, 2-16 at 70/71-79/80, 2-13 at 80/81-89/90, 4-11 at 90/91-93/94. Other regenerates still had a large, four-zoned growth region but with terminal anus or had not initiated metameric differentiation.

The data cited above explain, perhaps only in part, why it is so difficult to obtain information as to normal segment number in species of *Perionyx*. Three of the large athecal Almora worms had tail regenerates, at 32/33, 35/36, and 70/71.

Parasites. A colonial vorticellid-like organism is present on many of the Simla worms. Various sorts of much smaller protozoa, blue-green algae, and other organisms are present on the vorticellids. A similar epicuticular fauna and flora, but much more densely aggregated, was found on many Jubbulpore specimens of *P. millardi*. The epizoa and their associates spread from the substrate onto a regenerate (especially when cephalic) as it develops.

Remarks. The clitellum of two Simla worms probably had regressed after cessation of reproductive activity.

Almora worms were secured at the end of the dry season from a small area that had been kept quite moist by waste water. They were active and presumably had been able to maintain themselves in that state, without diapause, throughout the unfavorable period. Absence of spermatozoal iridescence, at that time of the year, may not be indicative of male sterility in an H morph.

P. bainii has been known hitherto only from the description of two types. Relationships are with *excavatus* rather than with *millardi*.

PERIONYX DITHECA Stephenson, 1931

This species is known only from the original account of four specimens from Thandaung, in the Toungoo Karen Hills. Spermathecal pores are at 7/8 on three of the types, at 6/7-8/9 on the fourth. The specific name suggests that the bithecal battery was regarded as normal for the species. Presence of extra spermatheca (hyperplasia) in species of *Perionyx* usually is associated with other evidence for cephalic regeneration. However, regeneration, in certain circumstances, often does result in a defective spermathecal battery. Relationships of *ditheca*, if one pair of spermathecae is normal, are with the Chin Hills *viridis* Gates, 1933. In spite of the distance between the two areas and the gap between, relationships appear to be close, *ditheca* distinguishable at present only by a slightly greater clitellar extent (through all of xviii instead of ending at 17/18) and absence of penial setae (possibly merely unrecognized?). If *ditheca* really is sexthecal, relationships to be considered are with *variegatus* (Michaelsen, 1907) from Darjiling district and *foveatus* from the Abor country farther to the east in the Himalayas. The Darjiling species is distinguished by a one segment shorter clitellum, wider separation of the spermathecal pores, a more anterior intestinal origin, and perhaps by presence of nephridial vesicles. Large seminal vesicles were said to be present in x but this requires confirmation. The geographically closer *foveatus* is distinguished by wider separation of the spermathecal pores, possibly also by presence of hearts in xiii and of a pair of female pores. Paired female pores are unknown in Indian species except after head regeneration and the genus is defined as having an unpaired pore. Hearts originally were said to be present in xiii but subsequent dissection of another specimen found last hearts in xii. Variation in location of latero-esophageal hearts is very rare in *Perionyx*, except after cephalic regeneration when it may be considerable, depending on level of regeneration, condition of specimen, etc. Other fragments of information (unfortunately too few though a number of specimens were available for study) also hint at a possibility of regeneration. Closer relationships may well prove to be with undescribed Burmese species unfortunately never obtained at a mature enough stage to warrant erection of new species.

Many hundreds of perionyxes were collected at various occasions over a period of years in the Toungoo Karen Hills in vain attempts to obtain further adults of *ditheca* and of *arboricola*

Rosa, 1890 (known only from a clitellate type found more than seventy years ago). Many thousands of perionyxes from other parts of Burma, secured during the season when most earthworms breed, also were too immature to warrant specific identification. In India, many hundreds of individuals were dug up from one site at irregular intervals during a period of more than a year in a futile attempt to obtain normal clitellate specimens of *millardi* (also cf. *P. simlaensis* below).

Clitellar tumescence of worms kept in the laboratory remained maximal (with occlusion of dorsal pores and obliteration of intersegmental furrows) only for a short period. Before long the clitellum disappeared when its site could be recognized only by color differences from adjacent regions, whiteness or a distinctly different shade of red. The literature provides good reasons for believing that few if any of the types of oriental species had a clitellum in maximal tumescence. Many may have been in a presexual stage (at which mature sperm often are recognizable on male funnels) or in a postsexual stage (at which spermatozoal iridescence usually is unrecognizable on male funnels and in spermathecae). At least 6 oriental species of *Perionyx* were erected on admittedly aclitellate specimens and just how juvenile some of them may have been is unknown — types of *dubius* were so young that spermathecae had not yet grown into coelomic cavities. Presumably then, maximal clitellar tumescence is attained rather quickly after which breeding soon is finished and then is followed by rapid regression of the clitellum. If sexual period is correlated with the monsoon cycle as in most oriental earthworms, it almost certainly is not, at least in Burma, earlier than in other genera.

PERIONYX EXCAVATUS Perrier, 1872

India

Pulta Waterworks, near bungalow, 0-0-1. Pulta Waterworks Survey. (Indian Mus.)

Pushok, hillsides near bungalow, December 1926, 0-0-82. S. L. Hora (Indian Mus.)

Gauhati, Assam, compound of Cotton College, March 1942, 0-0-2. P. K. Das.

Dehra Dun, United Provinces, October, 78-4-22. M. Matthur.

Almora, United Provinces, in wet ground near spring, at elevation of *ca.* 6000 feet, June, 0-0-15.

Philippine Islands

Manila, Sampaloc, garden, September 1958, 0-0-2. Magdalina Cantoria per Y. Kondo.

Fiji Islands

Suva, January 25, 1939, 0-0-1. Tree hole, May 20, 1945, 4-0-0. R. A. Lever per N. Tebble.
Tailevu, January 21, 1946, 0-2-0. R. A. Lever per N. Tebble.
Levuka, Ovalau, banana stem, November 12, 1945, 1-0-0. R. A. Lever per N. Tebble.

Hawaii

Honolulu. Semi-damp soil covered with plant debris and some animal faeces, dairy farm, University of Hawaii, May 23, 1956, 0-0-2. Very wet soil saturated with animal faeces along drainage canal, dairy farm, University of Hawaii, May 23, 1956, 1-1-14. J. E. Alicata.
Manoa Valley, Oahu, humus, banana plantation, March 8, 1959, 1-0-0. Y. Kondo.

External characteristics. Segments, in specimens without indications of posterior amputation or regeneration, 123, 128, 129 (small juvenile), 131 (2 specimens), 139, 140, 143, 145, 146, 147, 152, 153. Pigmentation red, restricted to dorsum except in front of clitellum where ventrum is invaded and increasingly so towards anterior end. Prostomium epilobous, tongue open. Nephropores, never obvious and often unrecognizable, near mL and close to margin of pigmentation, in a rather irregular rank on each side of body.

Male pores lateral and very slightly anterior to penial setae, usually recognizable only after removal of cuticle and when traction on the epidermis has separated the lips. Each pore, and its adjacent group of penial setae, is in a transversely elliptical white area, usually more or less raised and with a slight transverse cleft in which the tips of 4-9 penial setae are just barely distinguishable. The two rather indistinctly demarcated elevations do not quite meet at mV and are included in a common male field with a fairly distinct boundary anteriorly and posteriorly but not laterally. The field (except for the white areas) usually is greyish translucent and slightly depressed but occasionally is quite level or even slightly protuberant.

Internal anatomy. Pigment, associated with circular muscle layer except in preclitellar segments of very dark individuals in which considerable pigment is deposited in an outer portion of

the longitudinal layer, lacking just underneath the interseg-
mental furrows and very sparse for a short distance on each
side. No trace of the alternation of transverse bands of dense and
sparse deposition that is obvious after removal of the longitudinal
musculature is recognizable externally. Special longitudinal
muscle band at mD usually densely pigmented. Septa are deli-
cate, without marked muscularity. More or less obvious peripheral
thickenings, without characteristic shape, of several to a larger
number of consecutive septa beginning in the region from 15/16
to 20/21, have been noted in a number of specimens. The degree
of thickening varies considerably.

Esophagus very vascular in x-xii or xiii, widened and bead-
shaped in xiii, with fairly high irregular longitudinal ridges on
inner wall in xi-xiii or xiv, valvular in xv. Typhlosole lacking.
(Intestinal origin in xv and/or xvi?)

Dorsal blood vessel, single throughout, complete, bifurcates
under the brain, the two branches reuniting above the sub-
pharyngeal ganglion to become the ventral trunk. A supra-
esophageal trunk is present in vii-xii, bifurcated posteriorly
twice, one branch to the heart of xii, another passing through
12/13 to disappear into the anterior face of the esophageal widen-
ing in xiii. Subneural trunk, adherent to parietes, usually ap-
pears to turn laterally in xiv or xiii and then to pass onto gut in
xiii to join an extra-esophageal. Extra-esophageal trunks, median
to segmental loops of viii, pass onto gut about at level of 8/9 but
do not unite mesially. One of them usually appears to pass off
from the gut to the parietes and under the nerve cord into the
subneural behind the seeming lateral bend of that trunk. Some
portion of the subneural usually has blood and is quite obvious,
but empty portions often are unrecognizable in field preserved
material. Small vessels pass off from dorsal trunk in vi-ix, those
of vii-ix at least joining the ventral trunk and hence known as
lateral loops or hearts. Hearts of vi usually have been traceable
to the ventral trunk. A pair has been found in v in two specimens
only, in neither of which the vessels could be traced to the
ventral trunk. Large hearts are present in x-xii with obvious
blood-filled connections with the supra-esophageal but the
branches to the dorsal trunk are without blood, filamentous or
unrecognizable.

Nephridia avesiculate, rather small, ducts long and slender,
passing into parietes in a slightly irregular rank on each side of
body.

Male gonoducts, without epididymis, join ental ends of prostatic ducts. Seminal vesicles of xii are large and appear to extend through xiii or xiii-xiv but actually are confined to pockets of 12/13. One vesicle, usually that on the right side, is about a half or even less the size of the other. The vesicles are in contact dorsally though not in the median plane, but in spite of appearances never seem to be united. The vesicles of xi are partly or wholly surrounded by coagulum from which, in some field preserved material, they may not be distinguishable. The coelomic cavity of x also is filled with coagulum. The prostates are confined to xviii (noted in 50 specimens). The duct is embedded in the gland and an ental portion is sinuous or in one or two small loops. Penial setae have nine or more rather irregular circles of spines though these occasionally seem to be arranged in a spiral rather than in discrete circles.

Ovaries fan-shaped and sometimes folded like a fan, each with several to numerous egg strings. Spermathecae are of medium size and then reach up only to level of dorsal face of gut which is low or are large enough to nearly touch the dorsal parietes. The duct is shorter than the ampulla and has a fairly large lumen. Most of the sperm is present in club-shaped spermatophores that are thicker entally where the iridescence is centrally located. The narrowed portion is yellow, transparent, and this portion often is visible in an open spermathecal pore. The spermatophores are in the duct and an ectal portion of the ampulla. Small spaces in the wall of the duct near the ental end sometimes are recognizable. Presence usually is indicated by roughenings or protuberances of the outer surface that may have an appearance of clusters or of an annular band. One or two of the chambers may be enlarged and especially protuberant. Sperm sometimes has been found in the chambers.

Reproduction. Iridescence on male funnels usually is brilliant and indicative of profuse maturation of sperm. Iridescence is recognizable also in spermatophores (never found outside the spermathecae) as well as sometimes in the intramural chambers of the spermathecal duct. Reproduction, since sperm are matured and exchanged in copulation, is assumed to be sexual and biparental.

Spermatozoal iridescence is brilliant on male funnels of aclitellate individuals in which seminal vesicles had reached maximum size though spermathecal ampullae are undistended and prostates are not mature. Spermatozoa are lacking in the sperm-

athecae and evidence for copulation prior to development of the clitellum has not been found.

Regeneration. Posterior amputation is so common that determination of normal segment number is difficult. Half of the specimens in one series already had tail regenerates. Cephalic regenerates soon become indistinguishable from substrates except for the anomalies of internal structure that often result from epimorphosis and/or morphallaxis. The abnormalities of the two specimens described below probably arose in this way.

Abnormality. No. 1. All organs from spermathecae posteriorly, one segment in front of usual position. Presumably resulting from hypermeric regeneration (−1) at some level in front of the first spermathecal segment.

No. 2. Spermathecal pores at 8/9-9/10. Female pores in xv, xvi. Male pores in xix. Lateral hearts in vii-x. Latero-esophageal hearts in xi-xv. (Intestinal origin in xx?) Bead-shaped widening of esophagus in xvi. Testes and male funnels (with spermatozoal iridescence) in xi-xii. Seminal vesicles in xii-xiii. Ovaries in xiii, xiv and left side of xv. Gonoduct funnels in xiii of female size but with plications as in male funnels. Normal male funnels are present in both sides of xiv and xv. Male terminalia, in xix, normal. As in case of the first specimen none of the usual external indications of regeneration are recognizable. Hypermeric head regeneration (+1) presumably had been involved.

Remarks. An accurate characterization of two portions of the digestive system has not been achieved, in part perhaps because of condition of material and/or because of individual variation. A gizzard has seemed to be present in v or in vi, in about equal numbers of specimens, rarely in both v and vi and then with septum 5/6 apparently inserted about at its equator. A gizzard was not distinguishable, macroscopically, in other specimens. Intestinal origin doubtless is posteriorly in xv or anteriorly in xvi but insertion on gut of septum 15/16 was recorded in the laboratory notes as esophageal or intestinal for nearly equal numbers of dissections. Each of the above mentioned determinations was for a worm that could not be suspected of having regenerated, as gizzard location and intestinal origin often is variant after head regeneration.

The intestine often is narrowed in region of xvii-xviii, sometimes so much so that the portion in xviii appears to be valvular. Enlargement of the prostates as they become functional during

the reproductive season presumably considerably compressed the gut. At greatest compression determination of intestinal origin becomes even more difficult.

A whitish deposit on the parietes in several worms from the western Himalayas sometimes was separated into small bits that looked superficially somewhat like micronephridia. Shreds of disintegrated peritoneum that remain attached to the muscular layer also sometimes look superficially like micronephridia.

Small protuberances sometimes seen on preseptal necks of nephridia in postclitellar segments may be adventitious or rudiments of secondary nephrostomes.

The subneural trunk or any portion thereof that is completely empty may be unrecognizable in dissections.

P. excavatus seems to be equally at home in the lowlands of tropical Burma and in the Himalayas at elevations up to 9000 feet. This is most unusual for an earthworm. Although the species has been widely transported, successful colonization now appears to be restricted to tropical lowlands, from Madagascar east to the Hawaiian Islands.

PERIONYX HORAI Stephenson, 1924

India

Cherrapunji, Assam, along stream, Munbow side, 0-0-1. (Indian Mus.)

External characteristics. Diameter, 4 mm. Setae, present from ii, more closely spaced in ventrum than in dorsum: 36/viii, 45/xii, 44/xx, vii, ix/3-4, lacking or invisible ventrally on viii. Clitellum (? indicated only by whitening of epidermis), annular, from 12/13 to 16/17, intersegmental furrows, dorsal pores and setae present.

Spermathecal pores, very small transverse slits, on 7/8-8/9. Female pore, presetal, median. Vestibular aperture open, slightly longer than wide. Intersegmental furrows 17/18 and 18/19 visible on anterior and posterior walls of vestibulum which is continued anteriorly and posteriorly above the furrows. Roof cross-hatched by slight furrows into rather small tumescences and with a deep longitudinal groove at mV. Penial bodies, just lateral to the groove, 1+ mm. long, bifurcated ventrally. A deep (seminal?) groove on lateral or anterolateral face of each penial body, continuous with a shallower branch along each terminal digitiform lobe, passes up onto vestibular roof and then anterolaterally. Male pores, presumably minute,

closed and concealed by soil particles, were not found though prostatic duct was traced through parietes into anterior end of seminal groove.

Internal anatomy. Gizzard, wide, in v. Intestinal origin in xix (?), gut gradually attaining full width in xx-xxi.

Segment xi short, 10/11 and 11/12 held together by sticky coagulum so that the whole mass at first looked like a single muscular septum. Seminal vesicles of each pair united dorsally and hence horseshoe-shaped. Prostatic ducts, about 2 mm. long, an ental portion slender and u-shaped, ectal portion with muscular sheen and straight, passing into lateral face of vestibulum which is conspicuously protuberant into coelomic cavities of xvii-xix.

Spermathecal duct muscular, narrowed abruptly just at or within the parietes, with a short, thin-walled, non-muscular(?) neck entally. Lumen rather irregularly slit-like ectally due to presence of several high ridges, abruptly narrowed and eccentric entally, almost circular in section just below the neck where it is again widened. Seminal chambers very small, ovoidal to spheroidal and closely crowded in a nearly annular band (but with one fairly wide gap) around neck of duct. Six to eight apertures into duct lumen were found.

Reproduction. Spermatozoal iridescence was recognized in the seminal chambers. As sperm are matured and exchanged in copulation, reproduction is assumed to be biparental.

Remarks. The worm is strongly contracted and brittle.

The invagination containing the penial bodies is similar to that of certain species of *Eutyphoeus* and, as in those forms, is called a vestibulum.

The species has been known hitherto only from the original account of six aclitellate types. The gizzard was believed to be in vi. However, one of the two dissected worms was abnormal, possibly as a result of anterior regeneration. Aggregation of spermathecal seminal chambers into a single band rather than two rosettes does not, at present, appear to contra-indicate the identification.

The clitellum of the present specimen, which is from the type locality, very probably had not become especially tumescent though copulation obviously had taken place.

Spermathecal pores were at 7/8-8/9 in four of the types and that location was regarded as normal. Divergent locations in two specimens, at 6/7-7/8, and 8/9-9/10, could have resulted

from cephalic regeneration. Data as to location of other organs in those two worms could confirm the inference and might enable good guesses at level of regeneration. Again, it was fortunate that the two aberrant worms were not the only ones secured. Percentage of homoeotic individuals ($33\frac{1}{3}$ per cent) is high.

P. horai appears to be close to *P. simlaensis* from which it is distinguished by a distal bifurcation of the penes, the intersegmental location of spermathecal pores and, possibly, by a more deeply invaginate vestibulum.

PERIONYX MODESTUS Stephenson, 1922

India

Dumpep, Khasi Hills, Assam, under stones on the dried up bank of Wasarah Stream, 31/3/30, 0-2-18 (poorly preserved). J. L. Bhaduri. (Indian Mus.)

Dumpep, 0-8-0. S. L. Hora. (Indian Mus.)

External characteristics. Length, 94-206 mm. Diameter, 3-6 mm. Segments, 170-220. Pigmentation, red, though dorsum appears blue. Nephropores, whenever recognizable, just above ventral limit of pigmentation. First dorsal pore at 3/4 (1 specimen), 4/5 (21, on 18 of which a more or less pore-like marking present at 3/4), 5/6 (1). Clitellum, presumably not fully developed, indicated only by a slight reddening or whitening of the epidermis between 12/13 and 16/17. Setal formulae, as indicated below; no penial setae nor are any setae present between male pores ventrally.

TABLE 1

Setal formulae of *Perionyx modestus*

/ii	/iii	/viii	/xii	viii/	xix/		
44	44	42g	49	g	5g	6	First lot
46	44	49	50	48	11	10	
42	56	51	49	g	12	7	
41	43	36g	52	47	1g	8	
43	43	56	51	45	12	11	
40	45	49	51	49	15	8	Second lot
31	47	52	50	52	18	9	
43	45	56	56	48	16	6	
63	68	84a	60	54	16	7	
38	48	45	45g	44	14	7	
/ii	/iii	/viii	/xii	/xx			

g, gaps in setal, circle, follicle apertures recognizable or invisible.
a, setae, on this worm, unusually closely crowded dorsally.

Spermathecal pores not closely paired; each may have a protuberant and annular lip. Female pore presetal and median.

Male field usually transversely, occasionally longitudinally, elliptical, dislocating 17/18 anteriorly and 18/19 posteriorly, extending laterally into region of *FI*, definitely delimited by a slight furrow, flat and slightly raised, slightly or deeply depressed, occasionally especially so at mV. A transverse equatorial groove is deepened laterally and there contains, on each side, a short penis circular to elliptical in cross section, with the minute male pore on the flattened ventral end. These penes may be so deeply retracted as to be invisible even after separating margins of the groove and then can be found only by slitting open the prostatic duct. A penis (of one worm) is protuberant from center of each of two longitudinal cushions that are on the sides of an especially deep median depression of the male field. One cushion is transverse and with a ventral transverse slit on a worm that has no recognizable trace of cushion or penis on the other side. Setae and follicle apertures, quite unrecognizable midventrally between the penis, first visible laterally just at margins of the field.

Internal anatomy. Gizzard in v (9 specimens), however 5/6 appears to be (three worms) inserted at or near the equator so that the posterior half or less seems to be in vi. Intestinal origin apparently in xix (3) or xx (2). Circulatory system as in *P. miniata* Gates, 1945, except that the last hearts are in xiii (12 specimens).

Male funnels large, sometimes reaching nearly to level of dorsal surface of gut. Seminal vesicles, in both xi and xii, usually united above the gut and horseshoe-shaped. Prostates confined to xviii, ducts 4-6 mm. long, each usually in a U-shaped loop, with ental limb slender and white, ectal limb thicker and with muscular sheen.

Spermathecae, large, reaching into contact with dorsal parietes. Duct much narrower and shorter than ampulla, probably slightly muscular, not specially narrowed within the parietes but abruptly narrowed entally, with a transversely slit-like lumen. Surrounding the neck portion is a collar of small chambers. This can be removed, in some worms, without apparent damage to duct. The apertures into seminal chambers then seem to be on a thickening of the floor of the ampulla and in a circle around the larger opening of the ampulla into the duct (a result of some unusual relaxation or distention of entalmost

portion of duct?). Seminal chambers, in other worms, open into the ectalmost portion of the neck. Spermatozoal iridescence has not been recognized within any of the supposed seminal chambers though strands of very sticky, slightly iridescent material pass to the apertures.

Reproduction. Sperm are matured and exchanged in copulation. Hence, reproduction is assumed to be biparental.

Abnormality. Several specimens were homoeotic. At the middle of an uninterrupted gonad sequence, in one of the worms, there was a testis and male funnel on one side of the segment, an ovary and female funnel on the other side. The number of gonads, in each homoeotic, was greater than normal and the sequence was uninterrupted. Gonad ratios (testes:ovaries) were: 2:8, 4:4, 4:6. Ratio in normal specimens, in all species of the genus with but two exceptions, 4:2 (testes and ovaries separated by an agonadal segment). In regenerated heads, ovaries very often are more numerous than in normal and unregenerate worms. Internal organization of the Assam worms showed that the homoeosis originated after hatching and during regeneration of a lost anterior portion.

Regeneration. Organization of the homoeotics permits the following conclusions. Anterior regeneration in *P. modestus* is possible, and can be equimeric, at all levels back to 15/16 at least. All reproductive organs of the pre-intestinal region of the body, i.e., all except the male terminalia, develop, in appropriate conditions, in homomorphic head regenerates. In species with that much regenerative capacity, head regeneration is possible back into the last quarter of the body and can be expected in *modestus*.

A tail regenerate 13 mm. long is present on a 70 mm. substrate. The two larger specimens have tail regenerates, and other large worms are posterior amputees.

Parasites. Nematodes are present in coelomic cavities of x in two worms.

Remarks. This species has been known only from the original account of types that were not clitellate. Smaller ones, *ca.* 85 mm. long, were said to be sexual and if so may have been of the same species as the larger and more immature ones. If, however, worms were juvenile, taxonomically important characters might not have been recognizable. Aside from the smallness of the (juvenile?) spermathecae, the only important differences from present material are absence of penes (unrec-

ognized because of deep retractions?), and absence of a collar
of seminal chambers (also unrecognized or unrecognizable be-
cause not yet developed) on the spermathecal duct.

PERIONYX SIMLAENSIS (Michaelsen, 1907)

India

Saharanpur, United Provinces, October, 58 small juvenile, 477 medium
to large juvenile, 11 early aclitellate, 2 clitellate and 4 postsexual
aclitellate specimens. M. Mathur.

External characteristics. Length (strongly contracted) to
160 mm. Diameter (clitellate specimens which are slenderer
than the larger juveniles) to 6.5 mm. Segments to 200. Pig-
mented, dorsum red but often apparently dark blue anteriorly.
Prostomium, epilobous, tongue open (34 specimens), appar-
ently closed (1). First dorsal pore, at 4/5 (34), 5/6 (1). Setae,
present from ii, more closely spaced ventrally than dorsally, no
definite middorsal or midventral gaps in the circles. Setal
formula of the largest juvenile, 63/ii, 64/iii, 50/viii, 53/xii,
53/xx. In large juveniles and more mature specimens, viii/5-8,
xvii/4-7, xviii/0-1, xix/4-7. Small juveniles usually have 1-5
setae between rudiments of male pores, 1 (4 specimens), 2 (5),
3 (10), 4 (8), 5 (1). The setal circle is unbroken ventrally in
the smallest juveniles and rudiments of male pores are quite
unrecognizable. Nephropores, in somewhat irregular longitud-
inal ranks.

Spermathecal pores, minute, in longitudinal grooves extend-
ing back from 7/8 and 8/9 into viii and ix. Female pore
definitely single and median (1 specimen) and probably one
other, paired pores possibly present (1), unrecognizable on the
others. Male pores, presumably minute, but not recognized.
Male field as in Michaelsen's specimens except that cushions
bearing the penes may be on lateral walls of a deep depression
having a transversely rectangular aperture, the cushions nearly
in contact mesially.

Internal anatomy. Pigment, red, present in both circular and
longitudinal muscle layers, density markedly decreasing poster-
iorly in the longitudinal layer.

Gizzard, rather small, in v (20 specimens). Gut widened in
xiii-xvi, with fairly well developed calciferous lamellae in xiv-
xv, less well developed in xiii and in xvi, numerous small cal-
careous granules still present between lamellae of xiv-xvi or

(incomplete clitellate worm) xiv-xvii, when worms were dissected several weeks after preservation. Intestinal origin in xviii (5), xix (14), xx (2, including the incomplete clitellate). No typhlosole (20). The portion of the gut in xvii may be valvular or with low lamellae continued from xvi (especially in worm with intestinal origin in xx). The gut wall in ix or x-xiii is heavily vascularized.

Dorsal blood vessel, single throughout, bifurcates underneath the brain, the branches reuniting ventrally to form the ventral trunk. A small median branch may be recognizable above the brain. The subneural trunk is continued anteriorly to the region of the subpharyngeal ganglia where it bifurcates. A large branch passes off to right or left side in xiv or xv and in xiii becomes continuous with one of the extra-esophageals which of course are median to the hearts as they pass onto ventral surface of gut in x. Hearts of x-xiii latero-esophageal, the last pair in xiii (20). Hearts or segmental commissures of ix-viii are lateral. Commissures of v-vii may pass to the ventral vessel on one side or the other. Three pairs of vessels from the ventral trunk are recognizable between 4/5 and the anterior bifurcation. Nephridia avesiculate and, relative to size of body, rather small.

Holandric, the testicular coagulum of x usually, that of xi occasionally, appears to be within a cylindrical testis sac but the membrane covering the coagulum may be only loosened peritoneum. Seminal vesicles in xi and xii only (20 specimens). Prostates confined to xviii (20). Prostatic duct rather short, stoutish, bent into two u-shaped loops. Male gonoducts pass through the anterior portion of the gland to open into the ental end of the prostatic duct. No penial setae.

Abnormality. (No. 1) Spiral metamerism involving ii-v. (No. 2) Spiral metamerism involving xv-xvii. (No. 3) Spiral in middle of body, involving 31 segments, none of the abnormality recognizable ventrally. Other specimens may have had spiral or other metameric abnormalities in a postclitellar portion of the body as no attempt was made to check metamerism in that region. (Metamerism always has been checked, for many years, in an anterior portion of the body back at least to male pores or to clitellum if that is more posterior.)

(No. 4) First dorsal pore at 5/6. Spermathecal pores at 8/9-9/10. Female pore in xv. Male pores in xviii. Gizzard in vi, calciferous lamellae in xv-xvii, intestinal origin in xx, last hearts

in xiv. Small male funnel in xi on left side, testes and male funnels in xii-xiii, seminal vesicles in xiii-xiv, ovaries and female funnels in xiv. Prostates large but confined to xviii. Aclitellate.

(No. 5) First dorsal pore at 5/6. Spermathecal pores at 7/8-9/10. Female pores in xiv-xv. Male pores in xix. Segment xvi incompletely separated from xv on the right side, setal circle of xvi on that side represented only by a few scattered setae. Septum 15/16 lacking on right side though nephridia of xv and xvi are present on both sides. Gizzard in vi, calcareous granules between lamellae of xiv-xvii, esophageal valve in xviii-xix, intestinal origin in xx, last heart in xiv on left side. Testes and male funnels in xi-xii, seminal vesicles in xii-xiii, ovaries in xiii and left side of xiv. Aclitellate.

(No. 6) First dorsal pore at 5/6. Spermathecal pores at L7/8, 8/9-9/10, L10/11. Clitellum on xii-xviii. Female pore in xvi. Male pores in xx. Spiral abnormality involving xiii-xvii but invisible ventrally where segments were counted. Gizzard lacking. Testes and male funnels in xii, a rudimentary male funnel in xi, seminal vesicles in xiii, prostates in xviii if counted on right side, xix if counted on the left. Intestinal origin apparently behind the prostates? Ovary and oviducal funnel of left side one segment anterior to those of the right side.

Regeneration. Anterior amputees and recent anterior regenerates were found only among the medium to large juveniles in which group 3.7 per cent of the individuals had been affected. All anterior (as well as the posterior) regenerates were exactly at intersegmental levels. Number of segments in metamerically differentiated purely cephalic regenerates: 7 at 7/8 (2 regenerates), 8 at 9/10 (also with a tail regenerate at 74/75), 10 at 10/11, 11 at 11/12 (tail regenerate at 114/115), 16 at 15/16, 16 at 16/17 (tail regenerate at 142/143), 17 at some level behind xviii (2 regenerates one of which probably was far behind xviii). Segment size in some of these regenerates already was the same as in unregenerate worms of similar thickness and age. Though regenerative growth apparently had been completed, pigmentation still was clearly distinguishable from that of the substrate. Older cephalic regenerates, in absence of external or internal evidence of homoeosis or organ multiplication, would have been unrecognized.

One unusually interesting anterior regenerate (S-4) was mainly cephalic and normal except for presence on the ventral side slightly left of the median line of a white tubercle

bearing a slit-like aperture. The latter opened by a slender passage through the pharyngeal floor into lumen of regenerate gut which lacked a gizzard. The substrate, in this case, was a 43-segment fragment which appeared from its size, pigmentation and segmental characteristics to have been excised from a region well within the last quarter of the body, perhaps behind 150/151. The anal tubercle is the last vestige remaining from regularization of a regenerate that originally was a heteromorphic tail. A short and normal tail regenerate posteriorly also was present.

Many of the worms, prior to collection, had lost a posterior portion of the body: 31 per cent of the small juveniles, 28.7 per cent of the medium to large juveniles, 36.3 per cent of presexual aclitellates, 50 per cent of the clitellates, 100 per cent of the postsexual aclitellates. Healing of unregenerate worms sometimes had been enteroparietal but in many cases, especially at more anterior levels, an appearance of such healing was provided by median contact of margins of the last segment in such a way as to simulate a vertically placed anal aperture. Separations of those margins revealed a slightly depressed, circular cicatrix which was either quite imperforate or centrally punctured by a pin-point-like opening through apposed gut wall and thin cicatrix. Homomorphic tail regeneration obviously is possible (cf. Table 2) at any level behind 27/28. Two worms showed consecutive tail regeneration, at 52/53 and 75/76, at 66/67 and 106/107. Three distinct shades or grades of pigmentation were recognizable on each specimen, changing from one type to another at an intersegmental furrow. As other external stigmata of regeneration had disappeared even the most recent regenerates must have been old.

Reproduction. Biparental reproduction is assumed. Copulation and cocoon deposition may be limited to a short period at end of the monsoon rains. If so, two years may be required for attainment of sexual maturity, the dry periods being spent in some sort of a diapause. Evidence provided by specimens secured at end of the period of activity indicates that neither cephalic nor caudal regeneration is restricted to diapause or seasons of inactivity.

Remarks. Live specimens naturally relaxed can be expected to reach a length of more than 300 mm.

A male field is quite undemarcated in a very large majority of the specimens. A shallow transverse groove often is visible

ventrally at eq/xviii. A slight depression at each end of the groove presumably marks sites of male pores between which, and in the groove, tips of 1-3 setae usually are visible. The male field, at that stage of development, appears to be about as in the types of *P. modestus*.

Seminal vesicles were lacking in ix-x of all normal individuals. Coagulum in x may have been mistaken for vesicles but what could have been mistaken for vesicles in ix? Nothing else in the description of the types suggests abnormality.

One clitellate Saharanpur specimen is abnormal in the cephalic region. The head of the other was lost near 13/14 at time of collection. Four of the presexual aclitellates, those with best development of the male field, are abnormal. How much regression of sex organs there may have been in the postsexual aclitellates could not be determined. In these circumstances characterization of spermathecae and of male terminalia (especially with reference to presence or absence of a vestibulum) is inadvisable.

The description above is based on supposedly normal specimens. More variation is indicated in segment of intestinal origin and in the extent of a valvular portion of the esophagus, than, for instance, in most species of *Pheretima*. Nevertheless, it must be remembered that some of the supposedly normal large juveniles could have regenerated so long before collection and in such a manner that no indication of regeneration would have been recognized. While fasting, especially during regeneration more anteriorly, one or more segments at the beginning of the intestine sometimes become narrowed so much as to be externally undistinguishable from a contracted valve. Possibly histological differences can be found but microtome sectioning was not possible when the material was available.

P. simlaensis certainly appears at present to be very close to *P. horai*. Aside from the genitalia, closely related species are most likely to be distinguishable from each other by size, color, number of segments, pattern of pigment deposition and minor characters of that sort. Yet norms for most of those characters in a local population could not be determined even from a sample of 500 odd specimens. In a genus with such an unusually high regenerative capacity as *Perionyx* at least some knowledge of that capacity should be helpful in estimation of species norms and relationships, especially when a very few specimens of a supposedly new species are available. Epimorphosis in

combination with morphallaxis certainly provides a vast variety of organization some of which, it is hoped, will be recorded in a future publication.

TABLE 2

Levels of posterior regeneration in one collection of

Perionyx simlaensis

27/28	1 specimen	95/96-99/100	8
35/36-39/40	1	100/101-104/105	4
40/41-44/45	6 specimens	105/106-109/110	5
45/46-49/50	2	110/111-114/115	4
50/51-54/55	4	115/116-119/120	3
55/56-59/60	6	120/121-124/125	4
60/61-64/65	5	125/126-129/130	6
65/66-69/70	4	130/131-134/135	5
70/71-74/75	6	135/136-139/140	7
75/76-79/80	2	140/141-144/145	3
80/81-84/85	8	145/146-149/150	3
85/86-89/90	4	150/151-154/155	3
90/91-94/95	13	155/156-159/160	2
		160/161	1

Genus WOODWARDIELLA Stephenson, 1931

By definition, this classical genus is "purely meganephridial." In more modern terminology the excretory system is holonephridial or holonephric, each of the anlage in a pair of embryonic somites having developed into a single nephridium with a preseptal funnel, a postseptal looped body, and an external aperture in the epidermis of the metamere containing the postseptal portion. Typically, a pair of such nephridia (and no others) is present in each segment except the first and last. Interpretation of "nephridial tufts," when scattered micronephridia were absent (or perhaps only unrecognized because of minute size or poor preservation), as meganephridia, in the classical system, required inclusion of several small oriental species in the Australian *Woodwardiella*. One of those species, *bahli* (Stephenson, 1925) subsequently became the type of *Nellogaster* which is related to *Lampito*. Another species, *burkilli* (Michaelsen, 1907), went into *Nelloscolex* which is related to *Tonoscolex*. These four genera, though as yet little known and incompletely characterized are modern rather than

neoclassical, being defined, insofar as circumstances permitted, in accordance with new insights as to evolutionary conservatism and plasticity of somatic and genital systems in earthworms. (A genus, originally classical but now defined more adequately in the modern manner, is *Eutyphoeus* — *vide* Gates, 1959.)

Supposedly meganephridial tufts of *W. pumila* were found (Bahl, 1942) to be clusters of discrete micronephridia. The species, as then characterized, clearly did not belong in any of the modern genera and so had to go, in the unrevised major portion of the classical system, into *Notoscolex*. Excretory systems of the remaining oriental species of *Woodwardiella* still are as inadequately characterized as those of *bahli* and *pumila* originally were but presumably are meronephric regardless of size of nephridial tubules. (Meganephric is not synonymous with holonephric as meronephric systems may have one to several pairs of meganephridia, usually in addition to the more or less numerous micronephridia.) Accordingly, *W. hastata* (Stephenson, 1915) *sarasinorum* (Michaelsen, 1897), *uzeli* (Michaelsen, 1903), and *kayankulamensis* Aiyer, 1929, are now transferred to *Notoscolex*, primarily to avoid necessity of considering an Australian genus in future discussion of geographical relationships of oriental earthworms.

Genus NOTOSCOLEX Fletcher, 1886

The digestive system in this classical genus, without reference to caeca, typhlosoles and supra-intestinal glands, would have to be characterized as follows: Gizzard in v or vi. Calciferous glands (omitting any mention of structure) lacking or: one pair in xvi or xv-xvi or xv-xvii, two pairs in xi-xii or xiv-xv, or xiv-xvi, three pairs in xiv-xvi or xv-xvii, four pairs in x-xiii, five pairs in ix-xiii, six pairs in viii-xiii, etc. Intestinal origin in xv, xvi, xvii, xviii or xix. Little is known even about the major trunks of the vascular system. The excretory system, by definition, is required only to be micronephridial. All species probably are meronephric but some are "purely micronephridial." In others "various combinations of mega- and micronephridia" have been recorded. Furthermore, prostates are of at least two sorts: 1) Tubular (though with slight lateral branchings of the central duct that may be recognizable only in microtome sections) and presumably of ectodermal origin. 2) Racemose, of the pheretima sort and then presumably of mesoblastic origin. Distribution, omitting mention of isolated areas where introduced forms now

are domiciled, Australia and New Zealand, South India and Ceylon.

Such a congeries has no geographical justification and obviously is not based on the over-all similarity that is to be expected in species so closely related as to belong together in one genus.

The type species of *Notoscolex*, *N. camdenensis* Fletcher, 1886, is Australian. Though inadequately characterized for present needs, it is generically distinguishable from *pumila*. For the latter a new genus now is erected.

LENNOSCOLEX gen. nov.

Setae four pairs per segment, *d* gradually becoming more dorsal posteriorly, *a* and *b* of xviii penial (or lacking?). Quadrithecal, pores on 7/8-8/9. Female pore median and slightly pre-equatorial, on xiv. Male pores, common apertures of prostatic ducts and penisetal follicles, on xviii. Clitellum annular, dorsal pores occluded, intersegmental furrows obliterated, setae retained, on xiv-xvii at least. (Pigment lacking.)

Septa all present from 5/6. Digestive system with one esophageal gizzard in v, intestinal origin behind xv, without calciferous glands, caeca, typhlosoles and supra-intestinal glands. Vascular system with unpaired, complete dorsal and ventral trunks, paired extra-esophageals median to the hearts, a supra-esophageal trunk but no subneural (instead, a pair of posterior latero-parietal trunks?), and latero-esophageal hearts in x-xii or xiii. Excretory system meronephric and without nephrostomes, behind the clitellum with one pair per segment of clusters of four to six small exonephric nephridia. Holandric, seminal vesicles in xi-xiii. Prostates racemose, of pheretima sort, the ducts joined entally (?) by the vasa deferentia.

Type species. Woodwardiella pumila Stephenson, 1931.

Distribution. Presumably South India (Travancore and Cochin only?). Transportation responsible for domicile in Burma and Java.

Remarks. Definition is, of course, tentative.

Notoscolex minimus, peermadensis, kayankulamensis, travancorensis, all of Aiyer, 1929 and *tenmalai* (Michaelsen, 1910) appear to be candidates for inclusion in the genus.

The digestive system, except for the extension of the esophagus posteriorly, is very simple, perhaps primitive but the meronephry of the excretory system is very advanced.

LENNOSCOLEX PUMILA (Stephenson, 1931)

Burma

Ye, (Amherst), 0-0-2. K. John.

Bassein, September, 0-19-84. K. John.

Rangoon (Hanthawaddy), January 1931, 0-0-20, Various dates, 0-12-24. In marshy area across road from Cushing High School, 0-47-105. K. John.

Pegu, 0-0-2. K. John.

Regeneration. A young tail regenerate with dorsoterminal anus is present (1 specimen) at 78/79.

Remarks. Length of Rangoon worms, 70-90 mm., is unusual and may be due to relaxation during preservation or to softening during the period the worms have been in formalin.

Although all of the nephridia appear to have been characterized as "integumentary" and exonephric (Bahl, 1942, p. 34), the first of those two adjectives certainly seems inapplicable, at least to the preclitellar tufts which are located on anterior faces of septa and above the parietes. Some of such clusters, especially those of v-vi, when material in much better condition becomes available, may even prove to be enteronephric and with ducts opening into the pharynx.

Certain septal cell masses, one or two near each nephridial cluster of posterior segments, were thought (Bahl, 1942, p. 33) to be vestigial nephridia. If Bahl's assumption proves to be correct, the vestiges presumably would have been derived by longitudinal splitting in each of the two segmental anlage, such as is believed to produce the meromeganephridia of giant perionyxes in the Himalayas. Abortion of connections to the septa along with the preseptal necks and nephrostomes would then give the astomate condition prevailing in *pumila.* That astomate meronephry, regardless of method of evolution, now appears too highly specialized and possibly too nearly terminal to be in a direct line of ancestry to *Megascolex* and subsequently to *Pheretima,* even if there were no geographical contraindications.

Relationships now in need of investigation appear to be those of *pumila* with *N. minimus, peermadensis* and *kayankulamensis.* From *peermadensis, pumila* is distinguishable at present only by penisetal characters of unknown significance. Similarities of the Burmese worms to *kayankulamensis* already have been mentioned (Gates, 1942, p. 117). The excretory system of the Travancore species was thought by its author to be like that of

N. bahli. It is most regrettable that Bahl did not find opportunity to study these dubious species. All of the author's attempts to obtain collections of the Indian forms have been unsuccessful.

LENNOSCOLEX JAVANICA (Michaelsen, 1910)

The excretory system of this species never did get the requested characterization by Bahl. However, the anatomy as now known, is so like that of *pumila* as to make a transfer to the same genus seem advisable.

Like *pumila, javanica* obviously is exotic in Burma where it was introduced presumably quite recently and by man. Inclusion in *Lennoscolex* requires origin in South India (and perhaps Ceylon) where it has not yet been recognized.

Genus LAMPITO Kinberg, 1867

Studies of three somatic systems, digestive, vascular and excretory, in a peregrine species, enabled resurrection of this genus from the synonymy of the polyphyletic *Megascolex* and characterization more in accordance with modern requirements. Unfortunately, nothing has been learned since the genus was reinstated (Gates, 1938) about the endemic species, and various deductions as to overall similarity still require confirmation. Such data as were available, however, indicated evolutionary conservatism of somatic anatomy and greater plasticity of the genitalia. *Lampito*, in its various setal arrangements, shows that "a definite and natural line of demarcation in an evolutionary process" can constitute an arbitrary and unnatural taxonomic boundary unless all structure is taken into consideration to estimate overall similarity.

LAMPITO MAURITII Kinberg, 1867

Anadaman Islands

Haddo, January 1932, 21-4-2 and 3 fragments. (Indian Mus.)
Pahargaon, January 1932, 16-13-5, and some pieces. (Indian Mus.)
Aberdeen, Port Blair, South Andaman, May 1932, 12-3-5. (Indian Mus.)
Andaman Islands, September 1932-May 1933, 2-7-0. H. S. Rao. (Indian Mus.)

India

Nellore, Madras Presidency, September 7-10, 400-0-229. Helen Benjamin.
Udayagiri, Madras Presidency, September 11, 0-0-58. Helen Benjamin.
Kurnool, Madras Presidency, September 23-25, 139-53-64. W. D. Sutton.
Madras, December, 0-32-36. Dorothy Pearson.
Cuttack, Orissa, February, 0-9-14. H. S. Chaudhry.

Philippine Islands

Bataan, Luzon, 0-0-32. Leon Laplaize. (Eisen Collection, California Acad. Sci.)
Calayan Island, from ploughed field, 4(+)-1-0. (Eisen Collection, U. S. Natl. Mus.)
Pandacan, Manila, hog lots, Bureau of Animal Industry, 1954, 0-0-4. 1956, 0-0-2. P. Refuerzo.

New Caledonia

Tinchialit, at 2020 feet, October 1949, 0-0-1. L. E. Cheeseman per N. Tebble.

A single and median female pore is present on a number of specimens.

Pigment is present in the special longitudinal muscle band at mD. Extra-esophageal trunks, in some of the worms, are free from the gut all the way back through xii. Brain, connectives and subpharyngeal ganglia left in iii (2 specimens, once well forward), in iv (once) and then posteriorly, by a transverse section exactly along 3/4.

Ovaries, fan-shaped, with numerous egg strings which may have as many as eight ova. Ovisacs, small, acinous, with several ova.

Reproduction. Spermatozoal iridescence on male funnels and in spermathecae of most clitellate specimens indicated that sperm had been matured and exchanged in copulation. Reproduction accordingly is assumed to be sexual and biparental.

Abnormality. (Specimen No. 1) An extra small, atypical male porophore present on left side of xix. A penisetal follicle with setae but no prostate or duct is present in left side of xix. Two unidiverticulate spermathecae on the left side of ix are bound together by connective tissue. The right spermatheca of ix also has but one diverticulum which is anterior and bifid distally, as is the single diverticulum of the left spermatheca in vii. (No. 2) Two spermathecae on the right side of

ix, the median of which has but one diverticulum and that on the median side. (No. 3.) Spermathecae of vii lacking. (No. 4) Two spermathecae on the right side of vii, each with a single anterior diverticulum. (No. 5) Spermathecae lacking on left side of vii but two present on the right side. The median spermatheca has a single anterior diverticulum slightly bifid distally. (No. 6) Spermatheca of left side of ix lacking, the spermatheca of the right side with only one diverticulum and that anterior. (No. 7) Spermathecal pore, on left side, at 8/9. Female pores on xv. Male pores on xix. Gizzard in v or vi (?). Intestinal origin in xvi. Last hearts in xiv. Testes and male funnels in xi-xii. Seminal vesicles in (xii?)xiii. Prostates in xix. Ovaries in xiv. The spermatheca has a lateral diverticulum only. A long series of metameric abnormalities, including helicometameres, is present from xxvi posteriorly but none were recognized anteriorly. The homoeosis of this worm probably resulted from hypermeric regeneration (+1) at or in front of 10/11. (No. 8) Extensive series of spiral metamerisms beginning with xvii. (No. 9-11) Each has a helicometamere, unrecognizable ventrally, involving ix-xii. (No. 12) Quadrithecal, pores at 8/9, left side of 7/8, and in an equatorial groove on the right side of vii. Intersegmental furrows and metamerism apparently normal except as now noted. Setae, except for a, are lacking on the right side of vii, and on the right side of vi only a-d, f and h are present. At equator of vii, on the right side, a groove is present that looks much like an intersegmental groove. Slightly behind f on the right side of vi is a short, slight but definite transverse furrow which contains no pore. Stigmata of regeneration are unrecognizable but in various species usually do disappear shortly in head regenerates. Amputation presumably was in region of 6/7 and somewhat irregular so as to result in loss of the left anterior spermatheca and perhaps a major coelomic portion of the right one. During regeneration there was some elongation of the substrate behind the level of amputation. Then new intersegmental furrows were formed across the elongated region. Such portion of the right anterior spermatheca as had escaped amputation had been almost completely histolyzed but the right middle spermatheca originally in viii and now opening to the exterior through an equatorial pore in vii had undergone no recognizable change during its migration.

Remarks. Pahargaon juveniles are all small and presumably had been hatched shortly before preservation.

L. mauritii obviously is exotic in the Andaman Islands as also in Burma. The original home of the species doubtless is in a southern part of the Indian peninsula from which worms have been frequently and widely exported. Successful colonization appears to have been limited to tropical lowlands.

Genus PHERETIMA Kinberg 1867

Generic definitions in the classical system, like those of families, sometimes contain descriptive matter indicative only of range of variation as known before 1900. Such statements, of course, should have been recognized to be liable to continual change as new species are found. One example is provided by the characterization of spermathecal pores in the classical definition of *Pheretima* (cf. Gates, 1959, p. 238) which was taken up into the subfamily definition. Omitting further consideration of descriptive text, the classical *Pheretima*, in effect, was defined as follows: Setae, perichaetin. Gizzard, between 7/8 and 10/11. Micronephridial. Testes and male funnels enclosed in testis sacs. Prostates, racemose. The last character is uniquely diagnostic of the family to which the genus belongs. The gizzard character is imprecise. Micronephridial, however defined, can have little significance at any hierarchical level of taxonomy. Testis sacs, even testes and funnels, are lacking in some morphs of certain species. Surely, more anatomical uniformity than that ought to be expected in species so closely related as to belong together in a good genus.

The reproductive, of all systems, is by far the best known in all earthworm families. It also is the one most affected by intrageneric evolutionary changes. New, macroscopically recognizable, genital, characters-in-common are unlikely to be found in a genus as large as *Pheretima*. They must be sought in somatic systems.

Two digestive organs usually were mentioned by most authors in species descriptions. The gizzard often was said to be in ix, ix-x or even x which, in spite of appearances, is morphologically incorrect. Septum 7/8 always is present and inserted on the esophagus in front of the gizzard. Whenever septum 8/9 is complete it is inserted on the esophagus just behind the gizzard. If 8/9, 8/9-9/10, or even 8/9-10/11 are abortive segmental vessels from the dorsal trunk usually show that the gizzard developed in the portion of the esophagus belonging to viii. Presence

or absence of intestinal caeca usually was mentioned in the past. Although these caeca have no place in the generic definition, further information as to conformation and segment of origin will be of assistance in determining relationships of species. For other parts of the digestive system, esophageal valve, calciferous region of the esophagus, typhlosoles, etc., considerable information, derived from thousands of specimens, now is available. For those species that have been studied, all of the evidence from normal specimens is so invariable as to warrant the extrapolation indicated in the tentative generic definition below. Whether the slight variation in segment of intestinal origin that has been recorded is real or fictitious remains to be determined.

Much less information usually was provided about the circulatory system. No mention whatever of any blood vessel is to be found in one species description after another in various older contributions. Location of the last pair of hearts is the only character included in many other descriptions. The omissions never have been rectified for many species. The vascular system of *P. posthuma* was believed by Bahl (1921) to be characteristic of the genus but that assumption soon was shown to be incorrect as regards the hearts. Otherwise, and except for a gap in the ventral trunk of one species (see *P. elongata* below), uniformity has been found in the mass of material examined since 1923. In absence of any indications to the contrary, the vascular system now is characterized as in the tentative definition below.

Momentary observation of any live specimen enables one to note disappearance from sight and then reappearance, even of a major vessel, as it is emptied and refilled. Obviously, the volume of blood is insufficient to fill all vessels simultaneously. As a result, different portions of the system are empty after preservation and when empty may be unrecognizable or almost so in field preserved material. All or nearly all of the subneural trunk, for instance, often is not distinguishable. However, in a large enough batch, a specimen usually can be found in which blood is present in some part of the trunk, even in the preclitellar continuation. That anterior portion, as well as certain parts of other vessels, appears to have been unrecognized in the presumably better preparations, specially preserved in the laboratory, of the few earthworm species that were studied by morphologists. Their descriptions sometimes need to be supplemented or corrected from data provided in recent taxonomic contributions.

Our knowledge of excretory systems in *Pheretima* comprises results of Bahl's study of *P. posthuma* and several other unnamed but indubitably peregrine species. Conditions found in *posthuma* (Bahl, 1919) were assumed, as usual, to prevail throughout the genus. That may seem rather gratuitous as the genus supposedly comprises some 400 odd species. Material available to the taxonomist rarely is well enough preserved to warrant expenditure of the time and effort required to obtain the desired information. Specimens often are encountered in which structure is almost unrecognizable in the supposed micronephridia. The peritoneum occasionally has disintegrated so as to leave attached to the musculature scattered shreds superficially resembling micronephridia. Divergence from the *posthuma* norm presumably should be anticipated, if anywhere, in the supposedly primitive species for which Michaelsen erected the subgenus *Archipheretima*. However, no contra-indications to Bahl's assumption were recorded by any of those who have studied species of *Pheretima* during the last thirty years. If the excretory system is uniform throughout all species, the genus will have to be defined much as below.

All organs of the reproductive system, except ovaries, oviducts and clitellum, are now known to have disappeared in parthenogenetic morphs of various species. If *Pheretima* is to be defined, as *Eutyphoeus* was (Gates, 1959), without exceptions or the qualifications of the classical system, any mention of genitalia becomes impossible. Such few characters as now appear to be uniform in species with sexual reproduction are segregated in a separate paragraph. The large gaps in our knowledge of three very important somatic systems require that the definition be labelled tentative. Such designation will obviate, it is hoped, unnecessary erection of any genus merely because of some more or less unimportant anatomical difference.

All pheretimas collected in Burma west of the Irrawaddy-Sittang axis, with the exception of one series of a single species, probably have been listed in previous contributions. Many of the specimens secured after 1931 in the region east of the Irrawaddy-Sittang axis were not considered in the contributions of that period. Characterization of those worms became impossible when the author's records as well as the specimens, were destroyed in World War II. The loss is especially regrettable as the species are endemic, with interesting parthenogenetic polymorphism or geographical variation.

Tentative definition. Digestive system, without supra-intestinal and calciferous glands (calciferous tissues in low ridges that are not lamelliform in region of xiii?) but with a gizzard that develops in viii. Vascular system, with unpaired dorsal, ventral and supra-esophageal trunks, a subneural trunk adherent to the parietes, paired extra-esophageal trunks median to hearts, (latero?) esophageal hearts in some of segments x-xiii. Excretory system, meronephric — paired clusters of astomate nephridia in iv-vi with ducts opening into the pharynx — astomate, exonephric, very small, v-shaped parietal nephridia numerous in each segment back from iii — larger stomate nephridia with funnels in the same segment as body of tubule, on both sides of septa from xvi posteriorly, joining postseptal canals that pass to longitudinal, supra-intestinal excretory ducts opening at frequent intervals into gut. Setae, numerous, in a circle at equator of each segment from ii posteriorly. Ovaries fan-shaped and with several egg strings.

Male pores postclitellar. (Female pores intraclitellar?) Testes and male funnels enclosed in testis sacs. Seminal vesicles postseptal. Spermathecae diverticulate and pregonadal. Prostates, racemose, of mesoblastic origin, with ducts joined entally by the vasa deferentia.

Distribution. The Andaman Islands, the mainland of Asia from the Chindwin-Irrawaddy axis of Burma east through Yunnan and Szechuan provinces of China to include Korea and Japan, thence south to include New Guinea, Java and Sumatra. Whether any species are endemic in islands from the Marianas, Bismarck Archipelago, the Solomons and New Caledonia eastwards remains to be determined.

The generic range, as indicated above, comprises only areas where species are endemic. The peregrine forms have been carried almost everywhere by man and can be found today in greenhouses of North America, Great Britain and northern Europe, and in botanical gardens elsewhere in Europe. Nearly a score of species are now known to be domiciled outdoors in North America. Some of them also are present in Africa, South America, the West Indies, Australia, New Zealand, various oceanic islands such as St. Helena, Hawaii, etc. Hitherto there have been no records from Alaska, Greenland, the Sahara or Arabia.

PHERETIMA ANALECTA Gates, 1932

This species, as indicated below, may have arisen from an *andersoni*-like ancestor in which the GM series began at 18/19. Only the marking on 19/20 had been retained by most specimens from the range of subspecies *analecta*. Others (28 of 207 in 1932 collections) were variant, having a second marking of normal or reduced size at 20/21 or 18/19 (1 specimen) or a single normal marking at 20/21 (1 specimen). More interesting, however, were eight specimens on which the marking at 19/20 was halved so as to leave a small bit of unmodified epidermis at mV. In *P. a. rufula* on the Pegu Yomas across the Sittang valley from Toungoo, all markings have disappeared except the one on 18/19. That is now divided, each half circular to longitudinally elliptical and separated from the other by a space equal to 8-10 intersetal intervals. Further south on the Pegu Yomas, in subspecies *promota*, the genital marking at 18/19 has been retained without division but often is enlarged so as to reach beyond segmental equators of xviii and xix toward or even to 17/18 and 19/20. A similar origin may then be possible for the single large marking on the ten Thaton specimens of *andersoni* mentioned below.

PHERETIMA ANDERSONI Michaelsen, 1907

Genital markings of the two Amherst types on which this species was erected are anteroposteriorly short, rather spindle-shaped, centered exactly along six consecutive intersegmental furrows 19/20-24/25. Worms with similar markings (var. *typica*) were obtained in later years only at the type locality and at Chaungson. The markings, though usually six, were along 5-8 consecutive furrows of 18/19-26/27. Most of the worms hitherto referred to *andersoni* had fewer markings, of the same orientation (transverse to long axis of the body), but anteroposteriorly longer. Locations, again indicated by reference to intersegmental furrows though equators of two contiguous segments nearly were reached, one, two or three of 19/20-22/23, always on consecutive furrows when two or three markings were present. Distribution of these variant forms within a range comprising Mergui, Tavoy, Amherst and Thaton districts apparently was such as to contra-indicate further varietal names. A single genital marking present on each of ten specimens from Thaton (at northern end of the range) was so large that it

could have originated from union of two or three markings at 19/20-21/22 or 20//21-21/22 (but cf. *analecta* above). Spermathecal pores on one of the ten specimens were just behind rather than at intersegmental furrows. The evolutionary trend seemingly indicated by available records is reduction in number of markings associated with more or less enlargement of all that were retained.

An unidentified worm from the Kyaukmedaung region of Tavoy district, where *andersoni* had not been recognized, was distinguished from that species as follows: Size (110 by 5 mm.), somewhat smaller. Color, red instead of blue though pigment probably is the same. Spermathecal pores just behind intersegmental furrows. Genital markings, transversely elliptical, two pairs between equators of xix-xx and xx-xxi. Subsequent collections from the same area probably provided no further specimens (nor of typical *andersoni* for that matter). The worm is now regarded as a mutant in which the markings on 19/20 and 20/21 had been divided without loss of axial orientation. Supporting evidence for such a development is provided by a Mergui specimen in which the single marking on 20/21 was quite definitely dumb-bell shaped (also cf. subspecies *analecta* above).

The two types of *nemoralis*, collected in 1931, are of about the same size as *andersoni* but were distinguished by the red color and the presence of a pair of longitudinally elliptical markings centered at 20/21. None of the later collections from the Heinza Basin area contained similar specimens though more typical *andersoni* from the area had markings on 20/21 and 21/22. Types of *nemoralis* are now thought to be mutants of *andersoni* in which a single marking at 20/21 had been divided with loss of original axial orientation.

P. analecta, in the Salween district just north of Thaton and into the Karen Hills of Toungoo district now appears to have evolved from an *andersoni*-like ancestor presumably with a GM series beginning at 18/19. Differences from *andersoni* are few and if it were not for the size (50-124 by 3-5 mm. and 92-102 segments) which appears to be too small to allow copulation with any known individuals of *andersoni* (204-260 by 10-11 mm. and 120-134 segments) subspecies status would have been justified. Many specimens of *analecta* were heavily infested by several sorts of nematodes and gregarines but the parasites are unlikely to have brought about so much reduction in size.

P. velata Gates, 1930, present in Toungoo Karen Hills along with *analecta* but extending west into Karenni rather than Salween district, is of *andersoni* size or occasionally somewhat larger. Some heavily parasitized individuals were smaller than usual but were larger than all of the examples of subspecies *analecta*. Ecological requirements probably are similar to those of *andersoni*. The most efficient collector digging under the author's supervision obtained only one specimen at the type locality but in early morning, a month later, any number desired could have been gathered at the surface. Differences from *andersoni* are slight : Transverse banding of pigment in many specimens. Location of spermathecal pores (as rarely in *andersoni*) just behind intersegmental furrows. Enclosure of spermathecal diverticulum in a tough sac. Restriction of genital markings (an unpaired median or one pair) to region between equators of xvi and xviii. Interbreeding with *andersoni*, at least in Burma, is not contraindicated by size but is by the distributional discontinuity.

P. compta Gates, 1932, coexisting with *velata* in Burma but extending into Phre province of Siam, may have ecological requirements like those of *velata* and *andersoni*. Burmese specimens were immature (all secured in September, the usual breeding period in the plains) and were heavily infested with various sorts of parasites. Siamese adults were collected in November, perhaps at the surface after completion of cocoon deposition. Differences from *andersoni* appear to be of little importance except as to the genital markings which are always in three ranks at 18/19-25/26. No evidence for a tripartite subdivision of *andersoni* markings was found.

P. longicauliculata Gates, 1931, north of the *velata* and *compta* ranges and extending from Karenni (possibly also Kalaw to Taungyi), Kengtung and an adjacent portion of Yunnan to the Khun Tan mountains and Doi Sutep in Siam, is somewhat smaller (140-240 by 7-10 mm.) than *andersoni*. Differences again are slight except as regards the genital markings. These always are paired and transversely elliptical, at some or all of furrows 17/18-29/30. The markings are about the same as on the above-mentioned Kyaukmedaung specimen of *andersoni*.

P. labosa Gates, 1932, from the region of the Sino-Burman border north of Kengtung, like *andersoni* has unpaired genital markings, usually only one. This may represent union of two belonging at 21/22 and 22/23. All specimens, even those secured

in October, were immature. Differences from *andersoni*, absence of pigment, smaller size of organs and of body, are slight.

P. sonella Gates, 1936, again from the region of the Sino-Burman border but to the west and near Namkham, has a single genital marking between equators of xxii and xxiv that could have arisen by union of *andersoni* type markings belonging at 22/23 and 23/24. A similar union of two or three markings was suggested above for certain Thaton specimens of *andersoni*. The six northern specimens, in part abnormal, were preserved in alcohol that had bleached any pigment that may have been present.

P. choprai Stephenson, 1929, across the Irrawaddy River and to the northwest in Myitkyina district, is known only from two types also alcoholic. Pigment of the *andersoni* sort may have been present. Genital markings are circular or nearly so, at 21/22-26/27 (at 17/18 once) and like those of *andersoni* except that the marking at 21/22 is completely separated into two portions. Other differences from *andersoni* are: male porophores much larger; spermathecal pores apparently slightly larger though soma size is smaller and located just behind intersegmental furrows; a slight tumescence present in front of each spermathecal pore.

Genital markings of the above-mentioned forms are not slight epidermal modifications of the sort present in various other genera but are distinctly delimited. Furthermore, each is invariably associated with a mass of glandular tissues in vertical cords that usually (always?) is surrounded by a strong sheath. Markings invariably are present and just as invariably are restricted to a region comprising segments xvii-xxx. All of these species are closely related and could have evolved from a form very much like *andersoni*. That ancestral form, though by no means primitive, may have arrived in Burma before other pheretimas as the *andersoni* group and *feai* alone have gotten across the Irrawaddy-Sittang axis without assistance from man. Because of the invariability of presence or absence of genital markings in ranges that extend down nearly through the north-south limits of Burma, *andersoni* and *feai* are believed to be specifically distinct though there are no size differences to contra-indicate breeding. Except in the far north where the Salween and Irrawaddy Rivers were crossed, *feai* just gets into Burma in hills at the Siamese border. In Burma the two ranges must about meet at Kawkareik. Overlapping of ranges in Siam

is to be expected. Solutions to many of the problems posed by Burmese earthworms must be sought in the adjacent east. Unfortunately, little is known about the oligochaetes of those lands.

PHERETIMA ANOMALA Michaelsen, 1907

Abnormality. Clitellum reaches 17/18 on the right side. Segments xix-xxiii are involved in a helicometamere that terminates ventrally at each end. Three prostates are present on the right side, with pores on xix, xx, and xxi, the male deferent ducts of that side joining the duct of the anterior gland. Segments in which intestinal caeca arose, unfortunately, were not determinable.

PHERETIMA BIPORA (Beddard, 1901)

Seminal vesicles that were supposed to be present in segment x of the types undoubtedly are nothing more than dorsal portions of testis sacs, if not mere masses of coelomic coagulum. Hearts probably are present in xiii. Though types are extant they are of little if any value. *P. gemella* Gates, 1933 (types and all other specimens destroyed during the war) and *flocellana* Gates, 1949 (named in a manuscript submitted in 1941) probably differ from each other and from *bipora* mainly with respect to characters such as these: shape and location of preclitellar genital markings; sizes of pseudocopulatory chambers, penes and pseudopenes; shape of prostatic ducts. *P. gemella* and *flocellana* are now placed in the synonymy of *bipora*. Whether any of the differences mentioned above, or whether other characters such as number of pseudocopulatory chambers are correlated with distribution so as to permit recognition of geographical races, cannot be determined until lost collections are replaced. The number of pseudocopulatory chambers now appears to be larger in a southern portion of the Mergui district (Burma) that may be near the middle of the species range. Parthenogenesis is suspected in some portions at least of the range, though supporting evidence cannot now be presented.

Relationships probably are closest to *P. anomala* but neither species can be derived directly from the other.

Coelomic copulatory chambers are uncommon in species with manicate intestinal caeca. They have been recorded only from the Chinese *pacta* Gates, 1935, which has stalked glands opening to the exterior through small tubercles (like those of *diffringens*, *hawayana*, etc.) and the peregrine *schmardae* (of

unknown origin). Each of those species has retained the primitive spermathecal battery with pores at 7/8-8/9. Derivation from a quadrithecal form involves addition of a single pair of spermathecae in vii and then of another pair in v, associated at some time or other with loss of the pair belonging in ix. Early stages in evolution of copulatory chambers are shown by several species but for each of them there are geographical or anatomical contra-indications to close relationships with *birmanica*. If copulatory chambers evolve as rapidly as indicated by *papilio,* relationships of *birmanica* to species with superficial male pores ought to be considered. One species, the Burmese *defecta,* has a spermathecal battery like that of *birmanica*. To derive the latter from a form like *defecta,* but with spermathecal pores still on intersegmental furrows, only the following changes would be required: demarcation of a small circular area of epidermal modification around each spermathecal pore and withdrawal of the porophore into a shallow invagination with transversely slit-like lumen; invagination of the male porophore into the coelom and elongation of the smaller circular area containing the pore into a conical penial body.

PHERETIMA BIRMANICA (Rosa, 1888)

The typhlosole, in Dehra Dun specimens, begins in the caecal segment and in the next 11-15 metameres is low, opaque, yellowish, slightly thicker dorsally and hence triangular in cross section, with low vertical ridges on the lateral faces. Then for several segments the typhlosole occasionally seems to be completely lacking. Thence, to its end, the typhlosole is translucent and of rather nondescript shape.

Seminal vesicles of adults are small and appear to be juvenile. Information as to maturation and exchange of sperm no longer is available. Reproductive organ polymorphism has not been found (400+ specimens examined). Male sterility is suspected.

PHERETIMA DEFECTA Gates, 1930

This species was erected on an athecal posterior amputee with manicate intestinal caeca. Seminal vesicles were quite juvenile or rudimentary. Prostates were lacking but ducts and male porophores were present. Reproduction presumably would be parthenogenetic. The type belonged to an intermediate morph, of the fourth order if spermathecae and prostates had been eliminated concurrently, or of a fifth order if spermathecae had been

lost before the prostates. Male porophores were like those of *jacita* in some of eight subsequently secured individuals one of which had a diverticulate spermatheca of the sort present in *jacita*. Testis sacs were lacking in one of the specimens, a condition that has been found in several parthenogenetic morphs evolved in other species of *Pheretima*. *Pheretima jacita* Gates, 1931, the only other taxon with manicate intestinal caeca in the *defecta* area, has small but normally developed spermathecae, large seminal vesicles and prostates. Reproduction is assumed to be sexual and biparental as sperm are matured and exchanged in copulation. *P. jacita* then is of or very like the H morph from which the parthenogenetic intermediate morphs have evolved. *P. jacita* is suppressed as a synonym of *defecta*. If relationships are with Burmese species gross changes in the genitalia have been involved, in the spermathecal battery if with *manicata* and *canaliculata* Gates, 1932, in the male terminalia if with *birmanica* (*q. v.*).

PHERETIMA ELONGATA (Perrier, 1872)

India

Karachi, Sind, September, 0-3-0. K. N. Bahl. (Four specimens, unlabelled, may have been from the same locality.)

Poona, Bombay Presidency, garden of Ferguson College, 0-0-10. K. N. Bahl.

Kurnool, Madras Presidency, from black earth, September, 143-99-516. W. D. Sutton.

External characteristics. Some of the clitellate Kurnool worms are small for this species, 90-100 by 4 mm. Genital markings of Rewa specimens, in xix-xxiii (56 specimens), xix-xxiv (2). Spermathecal pores, minute and superficial, at 5/6-6/7, whenever present.

Internal anatomy. Pigment unrecognizable in special longitudinal muscle band at mD.

Dorsal blood vessel often apparently continued forward to a bifurcation just in front of brain, the two branches very shortly disappearing. However, within the tissues associated with the pharyngeal bulb, the real dorsal trunk — larger than the median branch just mentioned — passes forward to the brain underneath which it bifurcates, the branches reuniting above the subpharyngeal ganglion to form the ventral trunk. The latter is continued posteriorly into vii where it usually turns to run upwards on the anterior face of septum 7/8, either on

the right or on the left side. Occasionally the trunk bifurcates, both branches passing up on anterior face of 7/8, one branch always much larger than the other. The ventral trunk, in the smallest juvenile that has been dissected, at first appears to bifurcate in front of 7/8 but a slender, colorless (functionless?) filament continues on through the septum to a bifurcation at equator of viii. There each bifurcation very shortly widens (thence onwards filled with blood) and then branches several times, one of two larger branches joining the extra-esophageal trunk, the other opening into a ventral portion of the heart of ix below the white bulb. The posterior portion of the ventral trunk ends exactly, in every specimen, with the hearts of ix. Between circumpharyngeal connectives which are assumed to be segmental commissures of i and septum 4/5 two pairs of vessels open into the ventral trunk, one shortly behind the connectives, the other on the anterior face of 4/5. These paired vessels appear to be ventral remnants of segmental commissures of ii and iv, the large gap between indicating site of former junction of commissures of iii. A pair of thin red lines, just recognizable in that gap in the smallest juveniles that were examined, may be still unaborted portions of the usually missing commissures. Segmental commissures of v, on one or both sides, may still join ventral trunk in adults. Commissures of vi-vii, large dorsally, seem to have lost their connections with the ventral trunk. No vessels from dorsal trunk to gizzard were recognized and no trace of commissures of viii was found. The pair of commissures behind the gizzard, formerly thought to belong to segment viii (Gates, 1926, p. 450), is now attributed to ix. Commissures of x-xii always open into ventral trunk and dorsally into the supra-esophageal. Until dorsal bifurcations to dorsal trunk have been recognized and found to be functional, hearts of x-xii must be characterized as esophageal. Hearts of xiii are present and normal, incomplete ventrally or lacking. Incomplete rudiments, always dorsal, comprise a short stem or stalk from the supra-esophageal trunk of about the same thickness as a normal heart and a terminal spheroidal or pear-shaped portion that is much thicker and large enough to be in contact with both septa 12/13 and 13/14. The stem, from the supra-esophageal trunk is red or white but the terminal portion always is dark and filled with blood. No slightest trace of a ventral continuation was found even at the ventral trunk. The variation in hearts of xiii in a Rewa series of 58 normally

polythecal worms is shown in Table 3. Subneural trunk, adherent to parietes, often appears to pass out from under the nerve cord to right or left side shortly behind xiii. Actually, however, a slender and apparently functional continuation of the trunk often is recognizable for some distance in front of xiii, occasionally almost to anterior end of body. A branch passing off behind the seeming lateral bend of the subneural is called smaller though occasionally nearly as thick. Larger and smaller branches, in a specimen with no hearts in xiii, join an extra-esophageal trunk, but in 55 worms turn dorsally in xiii and open into the supra-esophageal trunk. Large and small branches, in specimens with hearts in xiii, join supra-esophageal in xii. Extra-esophageal trunks turn laterally and pass off from gut in xiii or xiv.

Typhlosole, simply lamelliform, beginning abruptly in region of xv-xviii (10 specimens), gradually becoming lower posteriorly, hinder half translucent, ending abruptly in 116th (of 187), 133rd (of 213), 137th (of 224) segments, in cxxviii (of a worm that had lost its tail well behind that segment), in lxx (worm with a six-segment tail regenerate at 98/99).

Spermathecal batteries, when present in Poona and Satna worms, are small 1-1 and 1-2, 1-1 and 2-2, 1-3 and 1-2, 1-4 and 1-1, or defective (1-0 and 1-1), Poona, all defective in Satna worms, 2-0 and 4-0, 0-2 and 0-4, 0-3 and 0-3, 0-2 and 0-0. A normally polythecal battery, a condition not hitherto reported from Indian material, characterizes each Karachi and many Rewa worms. Variation in numbers is shown in the table below. Spermathecae are lacking in most of the Kurnool worms. Thecal individuals from that locality have only one or two spermathecae at each of one, two or three of the normal four locations.

Reproduction. Data for sperm maturation and exchange in copulation no longer are available. Parthenogenesis and male sterility is anticipated in athecal individuals as well as in many of the worms with defective batteries.

Castings. Observations on casting deposition were made in a patch of sticky black earth, well shaded by a large tree, where *elongata* was the only species present. Tower-shaped castings never were found. Intestinal ejecta occasionally was in a single uninterrupted cord 2 mm. thick and 20-40 mm. long. More often cords were deposited in irregular piles 10-20 mm. high and 20-35 mm. wide.

Remarks. The vascular system of *elongata,* in an anterior portion of the body, is more divergent from the supposed generic norm than in any other species for which information now is available. Whether the deviations arose before or after appearance of parthenogenesis is unknown. Some of the little available evidence (as yet unpublished) that is provided by sexual morphs from the probable homeland of the species hints at a possibility that hearts may have been added in xiii after reproduction had become asexual. This might then mean that somatic as well as genital evolution can proceed more rapidly in asexual than in sexual forms.

P. stelleri (Michaelsen, 1891) and some of its inadequately characterized subspecies or varieties may have to go into the synonymy of *elongata.*

P. elongata has been widely distributed throughout the world, presumably by man. Successful colonization appears to have been limited to tropical lowlands. The original home of the species probably is to be found in islands to the southeast of the Asiatic mainland.

TABLE 3

Hearts of xiii in a Rewa series of *Pheretima elongata*

Both hearts present, complete and normal		34 specimens
One heart normal, one rudimentary		8
Right heart normal	7	
Left heart normal	1	
One normal heart present		5
On right side	2	
On left side	3	
Both hearts rudimentary		3
One rudimentary heart present		4
On right side	2	
On left side	2	
No hearts or rudiments		4
Total		58

TABLE 4

Variation in number of spermathecae in *Pheretima elongata* from Karachi and Rewa

Segment v	Segment vi	Specimens	Segment v	Segment vi	Specimens
2-2	1-3	1	3-3	2-4	1
2-2	2-3	2	3-3	3-2	1
2-2	2-4	1	3-3	3-3	13
2-2	3-3	3	3-3	3-4	2
2-3	2-2	1	3-3	3-5	1
2-3	2-3	1	3-3	4-2	1
2-3	2-4	2	3-3	4-3	1
2-3	3-2	3	3-3	4-4	2
2-3	3-3	6	3-3	5-4	1
2-3	3-4	3	3-4	3-4	2
2-3	4-3	3	3-4	4-2	1
3-2	2-2	1	3-4	4-3	1
3-2	2-3	3	3-4	4-4	1
3-2	3-3	2	4-2	3-4	1
3-2	3-4	1	4-3	3-3	2
3-3	2-3	3	4-4	4-3	1

"2-2" means two spermathecae on the left side, two on the right side, in segment v or vi according to the column.

PHERETIMA EXIGUA Gates, 1930

Seminal vesicles of adults are small and those of xi are included in the testis sac. Information as to maturation and exchange of sperm no longer is available. Prostates frequently are small, rudimentary or lacking. Individuals so characterized are of second order intermediate morphs evolving toward an anarsenosomphic stage (R morphs). Other morphs were unrepresented in collections comprising about 600 specimens.

Evolution towards an R morph is sufficiently advanced to warrant confident anticipation of parthenogenesis.

P. exigua does not appear to be closely related to any of the Burmese endemics. Anatomically, the species is nearest to *diffringens*, which may have come originally from some part of China or Japan.

PHERETIMA FACETA Gates, 1932

North Andaman, Andaman Islands, on the moist jungle path between Port Bonington and Base Camp, 24.xii.33, 0-0-1. H. S. Rao. (Indian Mus.)

External characteristics. Size, *ca.* 100 by 4 mm. Segments, 114. Pigmentation unrecognizable (alcoholic preservation). Prostomium epilobous, tongue open. Setae: 26/iii, 38g/viii, 48/xii, 53/xx, viii/16, xviii/10, xvii/14, xix/16. First dorsal pore, at 12/13.

Spermathecal pores minute (not slit-like), only slightly behind intersegmental furrows. Female pores possibly represented by two minute, grey spots close together on roof of a transversely slit-like depression. Male pores slit-like and of about the same size as the female pore depression, each at center of a small, transversely elliptical area surrounded by several concentric furrows. The furrowed area is slightly protuberant.

Internal anatomy. Septum 9/10 represented by a thin membrane inserted on gut behind heart of ix and attached peripherally to 10/11. Intestinal caeca simple, arising in xxvii and extending into xxiii. Typhlosole, which begins in caeca segment, simply lamelliform and at first not quite one mm. high. Only heart of ix (lateral) on left side, both hearts of x apparently esophageal, hearts of xi-xiii latero-esophageal. Lymph glands present behind prostatic segments.

Testis sacs unpaired, ventral, between nerve cord and ventral blood vessel. Spermathecal diverticulum passes into duct at parietes, the stalk portion sinuous or in very short zigzag loops.

Reproduction. Spermatozoal iridescence is obvious on male funnels and in ental portions of spermathecal diverticula. As sperm had been matured and exchanged in copulation, reproduction is assumed to be sexual and biparental.

Remarks. Markings like setae in follicle apertures are lacking or unrecognizable on i of this worm. Setae have however been found in the peristomium of head regenerates in species of *Perionyx*. Presence of setae in i also has been recorded for a Chinese species of *Pheretima*.

Location of spermathecal pores, in this specimen, is not as distinctive as in the types.

Ten specimens from Ponape, Natsushima, Truk Islands, in the Pacific have been referred to *faceta*. Some, if not all, were abnormal and parthenogenesis is suspected (spermathecae of viii often had no diverticula). The misidentified worms appear to be more like *P. javanica* (Kinberg, 1867) than *faceta*.

Protuberances on xviii warrant a suspicion that male porophores may be retractile into slight parietal invaginations.

PHERETIMA FEAI (Rosa, 1888)

These worms were not obtainable by digging over upper layers of soil but in early morning hours, at some time during October-November, vast multitudes crawl around on the surface until killed by heat or sunlight. They are so snake-like in appearance that coolies refuse to gather them, even for a considerable addition to the usual wage.

The worms are distinguishable at present from *andersoni* only by absence of genital markings and a slight but definite difference in color. They were suspected for some time of being merely a mutant population of *andersoni* restricted to a small area around the town of Kawkareik in the hills of Amherst district near the Siamese border. That was subsequently contra-indicated by individuals found on Mt. Kambaiti, far to the north and west of the Salween River, in an area where *andersoni* is unknown. Transportation from one locality to the other seems highly improbable. For the present, ornate taxa (i.e., with genital markings) are allowed to retain species status independent of *feai*. Nevertheless, absence of externally recognizable indications of geographical variation in so large a range (even if the two sites are at or near southern boundaries) now seems unusual.

Tropical soils are commonly thought to be poor in organic matter. Yet down below the layers usually dug over by collectors earthworms do find an adequate supply of food. So much, indeed, that all species living at those depths are of medium to large size; diameter when strongly contracted 6-15 mm.; length, when contracted, to 600+ mm.

PHERETIMA GLABRA Gates, 1932

This species, *tenellula* Gates, 1932, and *victa* Gates, 1936, respectively, are known only from the description of 24, 49 and 16 types. All specimens of *glabra* and of *tenellula* had large seminal vesicles and prostates but were athecal. As externally adhesive spermatophores are unknown in the genus, reproduction presumably is uniparental even though sperm are matured (cf. R morph of *P. anomala*). Each specimen of *victa* had one pair of spermathecae but seminal vesicles were small (juvenile or rudimentary), those of xi within dorsal extensions of the posterior testis sac. The spermathecal diverticulum probably was abnormally elongated (at least relative to length of main

axis) and without definite differentiation into stalk and seminal chamber. The main axis, though shorter than the diverticulum, may have been normally proportioned. Spermatozoa certainly were lacking in the spermathecae and testes probably were sterile. Seminal grooves are rare in the genus *Pheretima*. Those of the three taxa, like the genital markings or porophores on which they are located, differ mainly in amount of anterior extension from site of the male pore. *P. tenellula* and *vieta* are placed in the synonymy of *glabra*. Estimation of relationships is difficult as no evidence has been recognized that would indicate whether types of *vieta* are of an H_p morph or of some intermediate morph that already had lost one or more pairs of spermathecae.

PHERETIMA HOULLETI (Perrier, 1872)

India

Andaman Islands, September 1932-May 1933, 0-0-1. H. S. Rao. (Indian Mus.)

Bombay, August, 1958, 0-0-2. V. B. Tembe.

Philippine Islands

Sampaloc, Manila, September 1958, 1-11-9. Magdalina Cantoria per Y. Kondo.

External characteristics. Size (contracted), 75-85 by 2-4 mm. Segments (Philippines), 85, 89 (old posterior amputees), 98, 99 (3 specimens), 100 (3), 101 (3), 102; other specimens are recent posterior amputees. Pigment obviously present, the dorsum of two Manila worms appearing to be almost black. Prostomium epilobous, tongue open (20). First dorsal pore at 10/11 (20); whether a more or less pore-like marking at 9/10 (once at 8/9), sometimes indicated presence of a functional pore, was not determinable. Spermathecal pores about $\frac{1}{4}$C apart. **Female pore median (18).**

Internal anatomy. Pigment, reddish brown, restricted to dorsum, on inner face of epidermis, through circular muscle layer, on outer face of longitudinal muscle layer, sometimes dense in special longitudinal muscle band at mD, lacking or very sparse immediately under intersegmental furrows and around setal follicles. Pigment is present between the follicles though an equatorial band containing the setae often appears externally

to be unpigmented. The longitudinal muscle band at mD is distinct back from the first dorsal pore.

Intestinal origin in xv. Intestinal caeca, short, arise in xxvii and pass forward into xxiv or xxiii, dorsal and ventral margins more or less deeply constricted at septal insertions. Typhlosole, rudimentary in xv-xxvi, from caecal segment rather lamelliform but with low, vertical ridges laterally, ending abruptly in 63rd (of 99) or 65th (of 103) segments. Low segmental ridges running posterolaterally from the typhlosole do not end abruptly at level of hind end of typhlosole as they do in *posthuma*.

Dorsal blood vessel, complete, bifurcating under brain, branches passing ventrally and uniting over subpharyngeal ganglion to become the ventral trunk. Between that junction and septum 7/8 only five pairs of segmental branches from the ventral trunk have been recognizable, one of a pair sometimes apparently lacking. Only one of the segmental commissures of vi has been traceable to the ventral trunk in many of the worms. Segmental commissures of vii usually pass to the ventral trunk. Unaborted dorsal portions of commissures of viii pass to the gizzard, no remnants of ventral portions having been found. One heart of ix, on the right or the left side, obviously is lateral — directly connecting dorsal and ventral trunks. The other heart of ix which may be of the same size dorsally or much slenderer usually becomes almost filamentous (though sometimes still red) further down, the ventralmost portion joining the ventral trunk about opposite the unmodified heart of ix. Hearts of x-xiii appear to be latero-esophageal though blood usually is lacking in each of the dorsal bifurcations. Extra-esophageal trunks, median to segmental commissures, pass onto ventral face of gut in region of ix and thence posteriorly are close together but not in contact. The trunks often appear to turn off from the gut in xiii and to pass to the parietes on which they pass back to region of intestinal caeca as if posterior lateroparietal trunks. No evidence has been found, even in best preservation, of extension behind caecal segments. Subneural trunk, adherent to parietes, probably always complete but when empty in preclitellar segments almost or quite unrecognizable. Blood glands present in v-vi. Lymph glands, present behind xv, show considerable regional and individual variation in size. When large they are horizontally U-shaped.

Testes discoidal to nearly spheroidal. Little or no coagulum in testis sacs. Male funnels small but plicate. Male gonoducts,

straight or slightly sinuous just behind funnel septa (without epididymis), come into contact near 12/13 and appear to unite, the common duct passing into prostatic duct slightly below the ental end. Seminal vesicles, small, though rather soft of juvenile shape. Pseudovesicles, when present, quite rudimentary and in xiii-xiv. Prostates, large, well developed, xvi, xvii-xx, xxi, xxii, xxiii. Ducts, muscular, in a C- or U-shaped loop. Copulatory chambers with anterior and posterior glands.

Spermathecae, each with the usual stalked gland. Ampullae collapsed, empty or with but little coagulum ectally. Seminal chambers of diverticula translucent. Ovaries fan-shaped, with several to numerous short egg-strings.

Reproduction. Spermatozoal iridescence is lacking on male funnels and in spermathecae of all specimens as well as in a number of others (not listed above) that have been examined in recent years. Spermathecal ampullae of other specimens with clitellum at maximal tumescence may be distended by a coagulum that is translucent entally and opaque ectally but again without spermatozoal iridescence. Such worms probably are male sterile. If so, reproduction must be parthenogenetic, at least in many of the places to which *houlleti* has been transported. Determination of status and relationships of the taxon (cf. Gates, 1956, p. 222) awaits information as to anatomy of worms in the unknown original home presumably somewhere in southeast Asia. Male sterility, according to data now available from recently colonized areas, may have appeared shortly after acquisition of ability to reproduce parthenogenetically but before drastic modification of genitalia had gotten under way. Accordingly, further studies of variation in *houlleti* can be expected to provide clues as to the nature of the steps by which those modifications are brought about.

Castings. Individuals of this species crowded in earth around plant roots in small pots, during July and August at Allahabad, deposited much of the intestinal ejecta on the surface of the earth. Castings were irregular cords, isolated or in low piles. Tower-like castings were not found. Rangoon worms, kept in much larger pots where they were less crowded, did not cast on the surface. Deposition under ground probably is usual. Castings contained no macroscopically recognizable plant materials. The worms obviously are geophagous.

P. houlleti is one of the three species that Darwin seems to have held responsible for production of tower-like castings "in

extraordinary numbers" at Nice. Towers also are not deposited by the other two, *Perichaeta luzonica* (now *Lampito mauritii*) and *Perichaeta affinis* (now *Pheretima posthuma*). Tower-castings from Calcutta, supposedly erected by some species of *Perichaeta*, probably were produced by a species of *Eutyphoeus*, possibly *E. waltoni* (Michaelsen, 1907). Individuals of that and several other species of the genus have made tower-like castings under controlled conditions in the laboratory.

Remarks. A size of 100-135 by 5 mm. had been reached by some Jubbulpore specimens (already listed elsewhere) that probably were obtained at a site unusually rich in some sort of organic matter.

Tail pieces of 28-35 segments in the Manila lot probably had been autotomized. Similar tail portions of two worms as preserved had not yet been completely separated off. Autotomy, as in *P. agrestis* (Goto & Hatai, 1899), probably is easily induced and quickly accomplished. Live specimens should be picked up by the anterior end rather than posteriorly.

One copulatory chamber of each Bombay worm had a single GM gland on its posterior face. Other deviations from the characteristic *houlleti* norm, such as larger size of the Jubbulpore worms or presence of a second stalked gland on an occasional spermathecae, are not unknown. Penial bodies, when any question as to identification has arisen because of such deviations, always have enabled reference of the worm to one of the three closely related forms, *houlleti*, *campanulata* and *meridiana*. Dissecting out the penial body has not been attempted by most of those who have studied any of these forms but is not especially difficult. Recognition of typical characteristics of the penial body in microtome sections is likely to be far from easy.

Relationships of the *houlleti* group are with *P. virgo* (cf. below).

PHERETIMA ILLOTA Gates, 1932

This taxon is known only from the description of two athecal specimens, secured across the border in China. Seminal vesicles were small, if not rudimentary, probably juvenile. An A morph now warrants confident anticipation of parthenogenetic reproduction. As seminal vesicles are small, male sterility is suspected.

An A morph such as this provides few and but slight clues for determination of relationships. If male porophores are the

same as in the ancestral H morph they might be of some assistance. Although the only modifications of the porophores hitherto recognized in genital polymorphism are regressive, positive changes perhaps ought to be looked for as they have appeared during evolution of subspecies, i.e., in geographical polymorphism.

More intensive collection in the proper areas can be expected to turn up the intermediate morphs that will provide proof of relationships. Somewhat less confidently perhaps a sexual H morph can be anticipated (cf. *rimosa*).

PHERETIMA MALACA Gates, 1936

This species is known only from the description of 18 specimens obtained at two widely separated trans-Sittang localities. Spermathecae may have been normal in two of the types but in others were abnormal (3 specimens) or rudimentary (3). Seminal vesicles were juvenile or rudimentary, the anterior pair included in a testis sac. Prostates were small, confined to xviii. Testis sacs were paired or unpaired and then U-shaped or annular. No evidence of maturation or of copulatory exchange of sperm was found, though 17 specimens had a fully developed clitellum. Male sterility, and consequently parthenogenesis, is anticipated. *P. malaca* is much like *papulosa* (Rosa, 1896) which also has small seminal vesicles, the anterior pair enclosed in a testis sac. The major morphological difference between the two taxa is absence in *malaca* of the spermathecae that open at 5/6 and 7/8 in *papulosa*. Such a difference was long recognized as sufficient justification for specific distinction. However, it is now known that the first and last pairs of spermathecae in a sexthecal battery have disappeared from certain intermediate morphs evolved, in at least three species of *Pheretima*, since establishment of parthenogenesis. Until much more is learned about somatic as well as genital variation in *papulosa* in its still unknown original home, relationships with *malaca* may have to remain uncertain.

PHERETIMA MANICATA Gates, 1931

All specimens of this species secured from the lowlands of Amherst and Thaton districts (the earthworm fauna in the hills of those districts is almost unknown) have had small male poro-

phores, and also on xviii two longitudinal genital markings reaching or even crossing 17/18 and 18/19. As that combination of characters appears to be geographically restricted, var. *typica* is now considered to be a subspecies. In worms from the Toungoo Karen Hills north into Yunnan and west into Thailand, size of male porophores is variable and genital markings though not longitudinal are of various shapes and locations. These northern worms from higher elevations are easily distinguishable externally. They were previously known as var. *decorosa* which is now given status of a subspecies. The area in which *P. m. decorosa* was found is much larger than that of *P. m. manicata*. Quite possibly material destroyed during the war would have permitted recognition of more than one local race in the northern portion of the species range.

Anatomically, *P. manicata* is close to but one Burmese species, *arboricola* Gates, 1936. The latter is chiefly distinguished, aside from several minor characters, by presence of a sort of "creeping sole" in the ventrum. This development, in acaecal arboricolous forms was thought by Michaelsen to justify recognition of a subgenus *Planapheretima*. In *arboricola* the sole is associated with highly specialized manicate intestinal caeca. *P. vallata* Chen, 1946, from Szechuan Province (China) is distinguishable from *manicata* only by the spermathecal diverticula which are like those of *diffringens*.

PHERETIMA OSMATONI Michaelsen, 1907

North Andaman, Andaman Islands, on the moist jungle path between Port Bonington and Base Camp, 24.xii.33, 0-0-1. H. S. Rao. (Indian Mus.)

External characteristics. Size, *ca.* 185 by 8 mm. Segments, *ca.* 126 (posterior amputee?). Pigment probably is present, at least in dorsum of preclitellar segments, each seta in a small, longitudinal, unpigmented stripe that does not reach either intersegmental furrow. Prostomium epilobous, tongue open. Setae: vii/8, viii/10, xviii/10, (present ventrally on xvi?).

Spermathecal pores, minute, superficial, each at center of a small, smooth area of shortly elliptical outline, porophore possibly slightly retractile into parietes so as to produce appearance of a slit-like external aperture. Female pores unrecognizable.

Internal anatomy. Pigment, probably dark red. Septum 9/10, as previously, represented only by a ventral rudiment. Intestinal caeca simple, reaching forward only into xxvi or xxv.

Typhlosole simply lamelliform, 1+mm. high shortly behind its origin in caecal segment. Hearts present on both sides of ix (lateral); hearts of x large and apparently esophageal; hearts of xi-xiii latero-esophageal. Lymph gland, in each postcaecal segment, continued into a long and laterally directed lobe on each side.

Testis sacs unpaired and ventral, ventral blood vessel above or resting on roof of sacs, nerve cord well below sacs. Penisetal follicles, coelomic, strongly muscular, lateromesially flattened, coming to a point dorsally and of triangular shape, one just lateral and one just median to duct of accessory glands, the median follicle somewhat smaller. Soft, white and presumably glandular material apparently passes into parietes between lateral penisetal follicle and prostatic duct but a stalk was not distinguishable. Common duct of the muscular-stalked glands T-shaped, the horizontal limb thick and fairly straight, the leg of the T slenderer and in the parietes even more narrowed. Pseudovesicles of xiv fairly large, one containing a brown body.

Spermathecal duct narrowed within the parietes. A glandular collar is unrecognizable. Diverticulum passes into spermathecal duct at the parietes.

Reproduction. Spermatozoal iridescence on male funnels and in seminal chambers of spermathecal diverticula is brilliant. Reproduction presumably is sexual and biparental.

Remarks. Pigmented areas are barely recognizable because of alcoholic browning.

Genital markings and associated glands appear to be lacking.

Pheretima papilio Gates, 1930

A good series of this species was obtained at a site not far from the west bank of the Irrawaddy River in Prome district, somewhat south of the town of Prome. No village was nearby, though one had been there some years before. The worms were recognized by the collector, K. John, as belonging to *P. papilio* and he was able to mention the trans-Sittang localities at which he had secured specimens with similar spermathecal and male porophores. Transportation, presumably by man, must be responsible for the presence of that isolated colony well away from the region where it is endemic.

Specimens from the southern three of the four Tenasserim districts have been sufficiently uniform throughout that area to

permit recognition of var. *typica* as a geographical subspecies, *P. p. papilio.* A satisfactory morphological characterization must, however, await re-assembly of lost data. A northern subspecies, *P. p. hiulca,* can be morphologically characterized more adequately, by reference to invaginations in the male porophores and possibly also to those associated with the spermathecae. An intermediate stage in evolution of the male porophores is indicated by the only records now available (Gates, 1932) for Thaton district. More variation than in the southern subspecies is probable in *P. p. insignis.* Male porophores of worms in one section of the Pegu Yomas (var. *fracta*) may be in a somewhat less advanced stage than in the Toungoo Karen Hills of the Shan Plateau.

Within the limits of an apparently good species, invaginations have evolved in association with the spermathecae. Superficial male pores have become deeply invaginate. All that is needed to provide the sort of copulatory chamber characteristic of many species (cf. *birmanica*) would seem to be very considerable narrowing of the opening into the invagination.

Pheretima pauxillula Gates, 1936

This species is known only from the original description of 18 sexthecal worms with pores at 4/5-6/7. Seminal vesicles were small or very small (presumably juvenile or rudimentary), those of xi included within the testis sac. Sperm, in each spermatheca of the five dissected specimens, were lacking and testes probably were sterile. *P. digna* Chen, 1946, known only from the description of five types from Szechuan, is distinguishable only by the slightly greater length of the intestinal caeca and by the looping of the spermathecal diverticula. Absence of spermathecae opening at 4/5 "usually" is the only datum, except for inclusion of seminal vesicles in the posterior testis sacs, that would justify suspecting parthenogenesis. Certainly, variation in number of spermathecae is very much more common in parthenogenetic forms than in species with obligatory biparental reproduction.

Pheretima planata Gates, 1926

Siliguri, Bengal, India, compound of the Dak Bungalow, 30/xi/35, 0-0-2. (Indian Mus.)

This is the second record of this Burmese species from India, the other being South Cachar in Assam.

PHERETIMA POSTHUMA (Vaillant, 1868)

India

Udaipur, Rajputana, August, 0-0-5. M. M. Goil. 0-4-9. Ella MacLeavy.
Rawalpindi, Punjab, May, 0-8-4. F. G. Dickason.
New Delhi, July, crawling about on a road in a private compound after heavy rain, 0-0-79.
Jalla, Patna, Bihar, March, 0-9-4. R. C. Lacey.
Cuttack, Orissa, February, 0-0-15. H. S. Chaudhry.
Bombay, August, 1958, 0-0-6. V. B. Tembe.

External characteristics. Segments (Bombay specimens), 113, 114, 115 (2 specimens), 116, 117. (Cf. Table 6.)

Genital markings in the specimens listed above are in the usual situations, in the setal circles of xvii and xix. Variation in segmental location but not from equatorial position does occur. Markings in a small lot recently received from the Philippines are located as follows: in xvii and xix (3 specimens), lacking on one side of xix (1), an extra pair on xvi (1), an extra pair on xx (1). Location of the markings in an Allahabad series is shown in Table 5.

Internal anatomy. Pigment, within the circular muscle layer, present sparsely in the ventrum though recognizable externally only in the dorsum, is brown. The special longitudinal muscle band at mD, in relaxed as well as contracted specimens, is present and distinctly outlined back from 12/13.

Esophagus in x-xiii (relaxed specimens) with slight circular and longitudinal furrows that mark off on inner wall fairly uniform squares to produce a pavement block appearance (no ridges or lamellae). Intestinal origin in xv (15 specimens). Intestinal caeca, arising in xxvii (15 specimens), usually short, reaching to 25/26, into xxv, or rarely just into xxiv, margins often smooth. Typhlosole, from caecal segment low and simply lamelliform, ending abruptly (Table 6) in region of 88th-91st segments. From each side of the typhlosole in each segment behind xxx an obvious but low ridge (contracted as well as relaxed individuals) passes off posterolaterally and through three segments to a low ridge on floor of gut at mV. Posteriorly the ridges do not get that far around but end abruptly at level of hind end of typhlosole.

Dorsal blood vessel complete, in favorable conditions traceable forward to the brain where it bifurcates — the branches passing ventrally along median faces of circumpharyngeal ner-

vous connectives and reuniting over subpharyngeal ganglion to form the ventral trunk. Subneural trunk, nearly empty throughout in relaxed specimens, probably complete, adherent to parietes. Extra-esophageal trunks pass onto ventral face of gut at 8/9 and continue back into xiii at least, close to median line but without uniting. The trunks are, of course, median to hearts.

Prostates, though reaching through xvii-xix or xx are only medium-sized but apparently normally and fully developed.

Spermathecae, small to medium-sized. The characteristic papilla in an ectal portion of the spermathecal duct easily is disclosed merely by slitting duct open with a needle. Ovaries, fan-shaped, with several egg-strings.

Reproduction. Spermatozoal iridescence, in worms with maximal clitellar tumescence, usually is obvious on male funnels as well as in spermathecal seminal chambers and frequently is brilliant. Iridescence was recognizable on male funnels of four Bombay specimens and in all spermathecal seminal chambers of each specimen. Absence of mature sperm, whenever observed for a number of years, has been attributable to: immaturity, lysis of sperm after the reproductive season had ended, or to virginity. Reproduction, for the present, is assumed to be sexual and biparental. Nevertheless, retention of seminal vesicles in a condition that is juvenile in parthenogenetic forms, and the frequency of inclusion of vesicles in the testis sacs of xi, as in so many forms that are likely to be male sterile, warrant a suspicion that in *posthuma* parthenogenesis may be possible even if only optional as yet.

Abnormality. Left male porophore and prostate lacking in a specimen with an extra genital marking on the right side of xx. Male gonoducts of the left side come to an end in a vesicular widening just in front of 17/18.

Regional homoeosis of some specimens, that has been seen in the past, now is attributable, as in certain lumbricids, to halving of mesoblastic somites early in development.

Remarks. As many as 140 segments have been recorded at some occasion in the past for this species. *P. hupeiensis* which does have as many as 125-140 metameres has been mistaken, several times at least, for *P. posthuma.*

Pattern of genital marking, size, and location, insofar as intrasegmental position (equatorial, slightly median to male pore levels) and regional situation (restricted to segments be-

tween xiv and xxx) is concerned, now seems to be unalterable, certainly unchanged in the thousands of specimens that have been examined.

Caecal locations, often difficult to determine, may be able to show whether extra prostates occasionally present in xix are there because of splitting of mesoblastic somites at the 18th level.

P. posthuma obviously is exotic in India in spite of its wide distribution in the north and its commonness in the Gangetic plains. Accidental introduction, presumably by man, may be responsible for its presence in the lowlands of Burma. The original home of the species must be further east, perhaps in Thailand or Indo-China.

Relationships now appear to be closest to *P. fluvialis* Gates, 1939, and *P. juliani* (Perrier, 1875), little known species from Siam and Indo-China.

TABLE 5

Location of genital markings in Allahabad specimens of

Pheretima posthuma

On xvii and xix only		1520
Lacking on	left side of xvii	10
	right side of xvii	15
	both sides of xvii	1
	left side of xix	15
	right side of xix	13
	both sides of xix	0
	left side of xvii, both sides of xix	1
Extra marking on	left side of xvi	2
	left side of xx	12
	right side of xx	14

Lacking on	Present on	
Left side of xvii	Left side of xx	6
Right side of xvii	Right side of xx	6
Both sides of xvii	Both sides of xx	2
Right side of xvii	Both sides of xx and xxi	1
Right side of xvii	Both sides of xx	1
Both sides of xvii	Both sides of xx and xxi	1
Both sides of xvii	Right side of xvi, both sides of xx, left side of xxi	1
Left side of xix	Left side of xvi	5
Right side of xix	Right side of xx	1
Right side of xix	Right side of xvi	5
Total		1632

TABLE 6

Typhlosole termination and segment number in Allahabad

specimens of *Pheretima posthuma*

Typhlosole ends in segment	Atyphlosolate segments	Number of segments	Remarks
67	12	79	Posterior amputee
79	13+	92+	Young, unsegmented tail-regenerate
88	23	111	
88	24	112	
89	24	113	
90	14	104	Posterior amputee
90	23	113	
90	23	113	
90	24	114	
90	25	115	
90	26	116	
91	24	115	

PHERETIMA RIMOSA Gates, 1931

This species was erected on eight Kengtung specimens with really large seminal vesicles and prostates. Reproduction is assumed to be biparental as sperm had been matured and exchanged during copulation. The types were of an H morph. Records (many of them incomplete) are available now for but 116 specimens. Prostates, in many of the subsequently secured worms, were small or lacking (though ducts were present). Seminal vesicles were small and testis sacs contained only male funnels and discoidal, juvenile, presumably sterile testes. Such worms belonged to parthenogenetic, second-order intermediate morphs. Male porophores and prostatic ducts, in two specimens from To Noi, had almost disappeared. Male gonoducts attenuated posteriorly in forty To Noi specimens in which male porophores and prostatic ducts and male porophores were lacking. Variety *effeminata* was erected on To Noi worms. Two were of late, second-order intermediate morphs. Others were of an R morph. The Latin name is abandoned in favor of more informative terms of reproductive-organ and parthenogenetic polymorphism.

P. rimosa, like *alexandri*, *anomala* and *campanulata*, is a species in which a sperm maturing H morph co-exists along with one or more of the major morphs (A, R, AR, ARZ). Find-

ing of a similar H in other species with advanced major morphs
perhaps should be anticipated.

PHERETIMA VIRGO (Beddard, 1901)

This species has been known hitherto only from descriptions
of the original seven Siamese specimens. Prostates are small or
absent. Spermathecae are vestigial, usually represented only by
"extremely small" adiverticulate sacs. A diverticulum, when
present, is from the lateral side of the duct and looped. *P.
mendosa* Gates, 1932, was erected on 46 Burmese specimens
with spermathecal pores, copulatory chambers, stalked glands,
genital markings and penes as in *mamillana* but with quite
juvenile vesiculae seminalis, small or rudimentary prostates
and spermathecae more or less as in *virgo*. Types of *mendosa*
and of *virgo*, all sexthecal, belong to parthenogenetic, fourth-
order intermediate morphs in which evolution toward an AR
morph is well under way. The spermathecae in the sexthecal
battery of specimens referred to *P. mamillana* Gates, 1931, were
normal, with a looped diverticulum from the lateral face of the
spermathecal duct. Prostates appeared to be normal and pre-
sumably were functional. Method of reproduction is unknown
and information now available as to anatomy provides no clues.
As a full complement of normal and apparently functional
genital organs is present, *mamillana* must be close to if not
actually identical with the biparental H morph from which the
mendosa and *virgo* lineages have evolved. Both *mamillana* and
mendosa are suppressed as synonyms of *virgo*. Evolution of
polymorphism in *virgo* appears, from the data now available,
to be more advanced in a central portion of the range (cf. Table
7) where an A morph has been found and an AR morph may
be present.

Classical authorities rarely provided information as to size
of spermathecal pores and structure of the spermathecal duct
in the musculature of the body wall even when microtome sec-
tions had been made. Sometimes, indeed, the pores could not
have been seen as they were subsequently found to be elsewhere
than as originally stated. Removal of the cuticle often is
necessary to permit certain recognition of minute pores, and
dissection under a good binocular can provide data that cer-
tainly were not obtained from microscope sections. One of the
many instances of taxonomic value inhering in previously over-
looked organization is the following.

TABLE 7

Number of individuals of various morphs in collections of

Pheretima virgo

	Morphs			Locality	District	Country
A	H	I₄	AR			
—	2	—	—	Kinmunsakhan	Thaton	Burma
—	1	—	—	Kawkareik	Amherst	
—	11	—	—	Ye		
—	53	—	—	Heimza Basin	Tavoy	
—	251	3	?	Kamaungthwe	Tavoy	
—	203	+	?	Various	Tavoy	
2	1	+	?	Nyaungdonle		
—	111	46	—	Zowai	Mergui	
—	—	7	—	Tale		Siam
—	7	—	—	Kaki Bukit	Perlis	Malay States
—	7	—	—	Baling	Kedah	

A, Athecal morph. H, Hermaphroditic morph with full complement of reproductive organs, presumably normally developed.

I₄, Fourth-order intermediate morphs in which evolution toward an AR morph is under way. AR, Athecal and anarsenosomphic morph. +, Records destroyed. ?, Information presently lacking to permit certain distinction from AR morphs of *campanulata* and *alexandri*. Localities in north-south order.

P. virgo is very close to the *houlleti* group of species. Penial bodies are different from those of the *houlleti* group but have not been seen in full protrusion and need more precise characterization. Differences in size of spermathecal pores and in an ectal portion of the spermathecal duct are invariable. The duct, in each species of the *houlleti* group, narrows considerably within the body wall to open through a minute pore at tip of a very small conical protrusion into a parietal invagination. At copulation, the penis can be inserted only into a small transversely slit-like space. In *virgo*, the spermathecal duct and also its lumen widen considerably within the parietes and the duct opens to the exterior through a large transverse, slit-like aperture. A penis presumably can be inserted much more deeply than in the *houlleti* complex, perhaps far enough to deposit spermatozoa at or close to entrance of the diverticulum where they are to be stored until needed as cocoons are deposited.

PARTHENOGENESIS IN *PHERETIMA*

A characteristic iridescence on male funnels and in spermathecae of earthworms long has been known to indicate, in the first instance, presence of sperm matured by the animal itself,

in the second instance, presence of sperm presumably received from another worm during copulation. Examination, some thirty years ago (Gates, 1933) of 250 fully clitellate worms belonging to a single morph of one species and collected during the breeding season showed: That two individuals had produced a little sperm. The others not only had matured no sperm but had no organs in which to receive male gametes should copulation be attempted. Externally adherent spermatophores never were found.

Many endemics, in the monsoon tropics of Asia, breed only toward the end of the rainy season. It was, therefore, comparatively easy, by examination of many specimens collected throughout the breeding season, to determine that sperm probably never are produced by certain forms. The worms are, in fact, male sterile. By isolating anarsenosomphic individuals of *hilgendorfi*, Kobayashi (1937) proved that reproduction is indeed uniparental. Other experiments, except for some preliminary trials mostly with sperm-maturing forms, were prevented by World War II, and since then have not again been attempted.

Meanwhile much information had been accumulated about modifications in genital anatomy associated with male sterility and some of it (taken to India on the last boat to leave Rangoon before Japanese occupation) subsequently was published. Identical changes having been found in different species, a uniform terminology (cf. Gates, 1956) of "reproductive organ polymorphism" became possible. As the same variations were found in the genitalia of other species (cf. Gates, 1954), parthenogenesis could be deduced, even though sperm is matured profusely.

Species of *Pheretima* that are now believed to reproduce parthenogenetically are listed below. Inclusion in the first list does not necessarily mean that every individual of the species reproduces asexually. Nor does it mean that sexual reproduction cannot be obligatory for some individuals of the species. All that can now be said is that individuals do, or the individuals of some morphs must (because of male sterility or organ defects), reproduce parthenogenetically. Genital anatomy of species in the second list provides more or less justification for suspecting or anticipating parthenogenesis. Other names will be added in subsequent publications. Biparental reproduction

obviously is not as universal as would have been expected not so many years ago.

Parthenogenesis in species of *Pheretima*

Burma	*Elsewhere*
anomala	agrestis
alexandri	hilgendorfi
campanulata	hupeiensis
diffringens	levis
defecta	
elongata	
exigua	
glabra	
houlleti	
meridiana	
minima	
rimosa	
virgo	

Suspected or anticipated

bipora	bicincta
birmanica	esafatae
illota	garama
inclara	incongrua
papulosa	montana
pauxillula	pickfordi
robusta	renellana
sulcata	taprobanae
	upoluensis

Testis sacs frequently have been mistaken for seminal vesicles and relationships of sacs with vesicles of xi often have been erroneously characterized. In many such cases vesicles of xi probably are within an unpaired sac or paired sacs. Included vesicles usually are small, juvenile or rudimentary. If enclosure of vesicles by the sacs follows establishment of parthenogenesis, many names may have to be added to the lists. For each of the above taxa there is some additional reason for suspecting parthenogenesis.

DISCUSSION

The variation that has bemused oligochaetologists into erection of unnatural species now can be segregated into five classes.

1) Individual. Species very often were erected on a single type or a short series from a single locality. Even if more material was at hand, information about internal anatomy usually was obtained, perhaps sometimes because of museum regulations, only from one or two dissections supplemented by one or two series of more or less defective microtome sections. Today many of those species still are known only from the original descriptions. Others remain unnatural because all subsequent identifications were of specimens having just those characters recorded for the type or the original lot. More or less variant specimens, especially when from a distant locality, became types of other "species." Recent studies of Burmese and other oriental earthworms (also cf. Gates, 1957, for a similar finding in the Lumbricidae) have shown that characters by which species were defined often are among those most liable to individual variation. Twelve names, two in current use, are now known (Gates, in MS) to be synonyms of one widely distributed form. In contrast to possessors of many names are the congeries or complexes masquerading as species, presumably because important differences were attributed to varietal or individual variation. Especially regretted, in case of little known species, possibly on the way to extinction, is the failure to publish information about variation that must have been noticed while identifying worms for regional or population studies.

2) Anomalous. One sort results from modification of embryonic development presumably often induced (Gates, 1958) by environmental factors. *Allolobophora relicta* of the Lumbricidae is an illustration of a "species" erected on a type which can, with some justification, be called monstrous. Other sorts of anomalies result from presence of one or more of the kinds of parasites by which earthworms are infested often in large numbers.

3) Regenerative. Almost any species seems to be liable to more or less frequent loss of a taxonomically critical anterior portion of the body or some fraction of it. Restoration of the lost part, not exactly duplicated, and especially in case of a single specimen from a little known area, is believed to have enabled erroneous characterization of several species never since recognized. Probability of such error is greatest in genera like *Perionyx*, all species of which may have a high regenerative

capacity. This enables replacement of any portion of the pre-intestinal region or regeneration of a head (containing all organs of the pre-intestinal region) at any level except those way back in a small posterior section of the body. The diversity of structure after regeneration is now known to be so great that no two regenerates are likely to be identical even when produced at the same level and in the same conditions. Regeneration homoeoties are frequent and probably have not always been recognized as such.

4) Geographic. This sort of variation is, of course, not shown by the better known peregrine forms that have been transported by man throughout the world. Intensive studies of an areal fauna when made locally, as in South Africa (Pickford, 1937) and Burma, have revealed geographical races in various endemics. These, apparently, will have to be studied in recently unglaciated areas where the soil and other earthworm habitats remain less influenced by human activities. Considerable local collecting in areas such as New Guinea may be necessary before subspecies can be distinguished from species.

5) The variation that is now known to be possible after reproduction has become parthenogenetic. This method of reproduction permits, in subspecies as well as in species, evolution of numerous clones or morphs. Whether all of the specific names based on defective individuals of the more aberrant morphs ever can be placed with certainty in any synonymy now seems doubtful. Some anatomical modifications of the morphs also were made during evolution of various species. The reproductive system presently appears to be the only one that is changed during parthenogenetic evolution. Hence, the characterization of "reproductive organ polymorphism" which can be shortened to parthenogenetic polymorphism or even to genital polymorphism if parthenogenesis is understood to be basic.

The new systematics provides no criteria for species in animals that reproduce asexually. In earthworms, parthenogenetic strains now appear to have evolved recently from sexual forms presumably definable in accordance with ultra-modern requirements. Proof of the descent is provided, in better known cases, by intermediates linking even the most modified morphs to one that is normally hermaphroditic and sperm producing. Instances also are known in which adults of a male sterile morph are distinguishable from sexual worms only by the juvenile condition of their testes and other male organs. If considerable

proportions of the earthworms in various regions of the world are not to be left in an "ataxic" limbo as it were, species must be more than an interbreeding population, even in that far distant future when limits of interbreeding among these soil dwellers will have been discovered. A species, as understood herein, includes any population that meets breeding requirements and also all recently evolved strains, clones, morphs, that can be linked by intermediate stages to the sexual population.

The classical system of the Oligochaeta, regardless of original intention, eventually crystallized around two suppositions. 1) That genera and higher categories can be defined and arranged in straight-line phylogenetic sequences by a very few and often quite simple or generalized characters. 2) That other differences in structure (including all of the vascular and nervous systems) are phylogenetically meaningless and hence of little or no taxonomic importance.

Assumptions basic to the author's revisions of that system can be stated somewhat as follows: A species cannot be finally defined until extent of its individual and geographic variation throughout the entire range is known. (Obviously, then, for some time to come, definitions must be changed as more data become available.) Any generic definition necessarily is tentative and liable to modification until such time as all extant species have been found and finally defined. Species so closely related as to belong in a monophyletic genus should prove the relationship by a considerable amount of over-all anatomical similarity. Genera so related as to belong together in a subfamily still should have some anatomy in common. Species rather generally are distinguished by characters of systems most liable to rapid evolutionary modification. Genera are to be defined by characters less liable to change, subfamilies by others still more conservative.

The study of individual, anomalous and regenerative variation, as well as of genital and geographical polymorphism, shows conclusively that in earthworms the reproductive system is by far the most liable to rapid evolutionary modification.

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